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# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME XIV  
1957-1958

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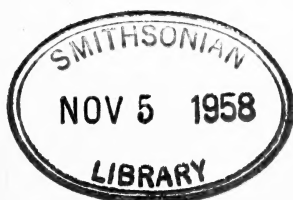
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Published quarterly by the  
California Botanical Society, Inc.  
2004 Life Sciences Building, University of California, Berkeley

Printed by Gillick Press, Berkeley, California





TO ROXANA STINCHFIELD FERRIS, Assistant Curator of the Dudley Herbarium of Stanford University, the California Botanical Society dedicates this, the fourteenth volume of *Madroño*.

Known affectionately to all of your many friends as "Roxy," it has been your lot to perform much "spade work" and to have reaped only that concealed reward of the personal satisfaction resulting from a job well done. We refer to the editing, and to the writing and rewriting and to the study of many groups of plants included in volumes II and III, and to your present considerable contribution of actual manuscript to the forthcoming fourth and final volume of Abrams' "Illustrated Flora of the Pacific States." Few authors have had such loyal and well trained assistance; few assistants have been so willing to suffer uncomplainingly the drudgery and heartaches that go into labor of this kind. We bring to you the affectionate greetings of our membership and wish you many more years of gratifying activity in Botany.

Bot.

CALIFORNIA BOTANICAL SOCIETY  
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REPORT OF THE TREASURER FOR 1957

RECEIPTS:

Balance on hand in commercial account, January 15, 1957.....	\$ 840.30	
From memberships and subscriptions.....	1,987.06	
From sales of back numbers of <i>Madroño</i> .....	58.00	
Receipts from annual dinner.....	211.75	
Received as authors' share of publication costs.....	360.00	
Contributions to memorial fund.....	75.00	
		<hr/>
Total receipts .....		\$3,532.11

DISBURSEMENTS:

Credited to endowment fund from sales of back numbers of <i>Madroño</i> .....	\$ 58.00	
Credited to memorial fund.....	75.00	
Cost of annual dinner.....	177.75	
Corresponding Secretary's expenses.....	45.86	
Editorial Secretary's expenses.....	10.00	
Dues payment, Strybing Arboretum Society (1957).....	5.00	
Refund on over-payment of authors' share of publication costs	15.00	
Cost of printing, binding, and mailing <i>Madroño</i> , Volume 13, Numbers 5, 6, 7, and 8.....	2,200.38	
		<hr/>
Total disbursements .....		\$2,586.99

BALANCE ON HAND IN COMMERCIAL ACCOUNT, American Trust Co., Palo Alto .....	945.12
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ENDOWMENT AND MEMORIAL FUND:

Palo Alto Mutual Savings and Loan Association, on hand January 15, 1957.....	\$4,586.47	
Accrued interest .....	172.15	
From sales of back numbers of <i>Madroño</i> .....	58.00	
Contributions to memorial fund.....	75.00	
		<hr/>
		\$4,891.62
American Trust Company, savings account, balance Janu- ary 15, 1957 .....	\$ 380.06	
Accrued interest .....	11.47	
		<hr/>
		391.53
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Total Endowment .....		\$5,283.15

Accounts audited and found correct:

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## ERRATA

- Page 3, following line 35 insert: of order Parietales, in the Englerian system.  
Dilleniaceae.
- Page 40, line 15: for Peirce read Pierce.
- Page 40, line 19: for Taris read Tario.
- Page 70, line 32: for (law-w) read (lav-w).
- Front cover, vol. 14, no. 3, line 6: for *Minulus* read *Mimulus*.
- Page 96, line 20: for Robert read Rupert.
- Page 115, line 5: insert Idaho in front of Elmore County.
- Page 147, line 1: transpose right and left.
- Page 153, line 34: for 3—dm. 7 read 3–7 dm.
- Page 218, line 35: for 1956 read 1957.
- Page 225, line 10: for saggitate read sagittate.
- Page 232, line 34: for no read so.





# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 1

JANUARY, 1957

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PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

# MADRÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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## FORECAST OF A SYSTEM OF THE DICOTYLEDONS

HERBERT F. COPELAND<sup>1</sup>

A standing problem of taxonomic biology — its importance and difficulty made known by the incompletely successful efforts of fully two centuries — is that of the natural and convenient organization of the families of dicotyledons in groups of the category of orders. De Candolle (1813; to him, what we call a family was an order, and what we call an order was a subclass, legion or cohort) remarked of this problem, "C'est là le problème le plus important à résoudre qui se présente aujourd'hui dans l'étude des rapports naturels." And Schnarf (1933) had still to say, "Dagegen ist die Gruppierung der Familien zu Ordnungen oder Reihen schon mit einer gewissen Unsicherheit behaftet, die darin zum Ausdruck kommt, dass die Abgrenzung der Ordnungen von verschiedenen Forschern vielfach in verschiedener Weise vorgenommen wird."

In his work just cited, De Candolle observed that there had been almost as many systems as systematists; which is not far from saying that every systematist has a right to his own system. Among the very many systems which systematists have produced, few have had much influence. During the nineteenth century, the system of De Candolle (of which that of Bentham and Hooker is a variant) overshadowed all others; subsequently, the system of Engler and Prantl has had the same effect. All this is as it should be. We need at every time to have an accepted system, by which we may know where to look for what concerns us in herbaria and manuals. The systems which have been offered as challenges to the accepted systems have brought about minor improvements in the latter. They have had the more important effect of keeping us aware that the accepted system is never the final truth. As the system of Engler and Prantl displaced that of De Candolle, so surely it will be displaced by one which is recognizably a more satisfactory representation of the system which exists in nature.

Considering these things, I took a summons to appear in a symposium as occasion to try to predict the system of the future; this to the extent of formulating the skeleton of a system which is set forth below.

This system gives much weight to microscopic characters, though I can scarcely claim mastery of the great mass of available data. Metcalf and Chalk (1950) give a bibliography of about twenty-five hundred titles, nearly all of them subsequent to the translation of Solereder by Boodle and Fritsch (1908). Schnarf (1931) listed about seventeen hundred contributions to embryology. Wodehouse (1935) listed some three hundred

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<sup>1</sup> It was a high honor, accepted with diffidence, to be asked to speak on "Anatomy and taxonomy" in a symposium commemorating the fiftieth anniversary of the Botanical Society of America, on August 28, 1956, at the meeting of the American Institute of Biological Sciences at the University of Connecticut. The present paper is a revision of the one given on that occasion.

papers on pollen grains, and Erdtmann (1952) about eleven hundred in the same field. Where study of vascular anatomy, at Harvard and elsewhere, has yielded definite conclusions, it has been possible to formulate orders with considerable confidence; for the rest, the orders are those of Engler and Prantl with certain amendments suggested by embryological or palynological data.

Large orders are preferred to small: in maintaining an order of two or three families, one is not far from leaving the families unplaced. However, it has not been found possible to be consistent in this matter. It is not considered necessary that the orders be definable by description.

Names are applied to the orders according to the principles of priority and typification. The experience of very many taxonomists has shown it necessary to apply these principles in dealing with genera and species. Experience with the formulation and naming of higher groups has been comparatively scant. Perhaps for this reason, taxonomists in convention have taken the position that it is possible to make defensible choices among the fairly numerous names which have been applied to higher groups without recourse to the principles cited. Whether or not this position is sound, no novelties are here added to the synonymy of ordinal names.

#### Subclass DICOTYLEDONES Lindley

Synops. British Fl. 4 (1829).

Order 1. MULTISILIQUAE L. Gen. Pl. ed. 6 (1764). Orders *Piperitae* and *Coadunatae* L. op. cit. Orders *Piperinae* (Brongniart, as class) and *Polycarpicae* (Endlicher, as class) Braun in Ascherson Fl. Brandenburg 1: 36, 47 (1864). Orders *Piperales* and *Ranales* Engler Syllab. 93, 106 (1892).

Among names of the three natural orders in which Linnæus placed these plants, that of which the apparent typical genus is *Ranunculus* is preferred to those of which the apparent typical genera are respectively *Piper* and *Magnolia*.

This order includes the generality of dicots with apocarpous flowers, as well as some of their immediate derivatives. They have been studied extensively by Bailey and his associates (Bailey and Nast, 1943, 1944, 1945; Bailey, Nast, and Smith, 1943; Bailey and Smith, 1942; Bailey and Swamy, 1949; Smith, 1943, 1945, 1946, 1947; Swamy, 1949; Swamy and Bailey, 1949). These scientists are authority for the assemblage here of a large number of families, including the Piperaceæ and their immediate allies. To current botanical opinion, this is definitely the primitive order of flowering plants. Some families are homoxylous, *i. e.*, having wood without vessels, in contrast to the heteroxylous condition which is characteristic of flowering plants. In some families the pollen grains are monocolpate, *i. e.*, marked by a single groove; this character they share with the generality both of the lower seed plants and of the monocots, while in typical dicots the pollen grains are tricolpate or of more elaborate types derived from this. The two primitive characters mentioned, and the peculiar

anatomical character of oil cells in the tissues, are distributed among the families of Multisiliquæ each one in seeming independence of the others. This means that, quite as one would expect of a primitive group, the families are isolated or fall into isolated blocks. It is necessary as a matter of convenience to maintain the order as a whole; it is not possible to divide it into a small number of natural orders. The families are as follows:

- a. Homoxylous, pollen monocolpate: Winteraceæ.
- b. Heteroxylous, pollen monocolpate: Degeneriaceæ, Himantandraceæ, Magnoliaceæ, Anonaceæ, Eupomatiaceæ, Myristicaceæ, Canellaceæ, Monimiaceæ, Gomortegaceæ, Lauraceæ, Hernandiaceæ, Lactoridaceæ, Calycanthaceæ, Chloranthaceæ, Piperaceæ, Saururaceæ.
- c. Wood degenerate, pollen monocolpate: Nymphæaceæ (pollen tricolpate in subfamily Nelumbonoideæ).
- d. Homoxylous, pollen tricolpate: Trochodendraceæ, Tetracentraceæ.
- e. Heteroxylous, pollen tricolpate: Eupteleaceæ, Cercidiphyllaceæ, Illiciaceæ, Schisandraceæ, Berberidaceæ, Menispermaceæ, Lardizabalaceæ, Ranunculaceæ.

Order 2. JULIFLORÆ (Endlicher as class) Braun in Ascherson Fl. Brandenburg 1: 62 (1864). Order *Amentaceæ* of Linnæus and Jussieu: one would not maintain a name in *-aceæ* as that of an order. Tippo (1938), on the basis of studies of the anatomy of the wood, assembled the families Hamamelidaceæ, Platanaceæ, Myrothamnaceæ, Stachyuraceæ, Betulaceæ, Fagaceæ, and Casuarinaceæ, as a natural group derived immediately from Multisiliquæ.

It is an annoyance to have no definite opinion as to the natural place in the system of the familiar families Salicaceæ and Juglandaceæ. Gundersen (1950) grouped Juglandaceæ with Myricaceæ and Rhoipteleaceæ, which may well be sound; but there is not much to tell where the group belongs.

Order 3. SCABRIDÆ L. Order *Urticæ* Jussieu, the mere plural of a generic name. Order *Urticinæ* (Bartling as class) Braun. Order *Urticales* Engler Syllab. 95 (1892). Ulmaceæ, Eucommiaceæ, Moraceæ, Urticaceæ. Study of the woods by Tippo (op. cit.) was held to confirm this generally-accepted group as natural, and to show that its origin was from the lower Julifloræ.

Order 4. GUTTIFERÆ Jussieu Gen. Pl. 225 (1789). Suborder *Theineæ*, Theaceæ, Marcgraviaceæ, Caryocaraceæ, Medusagynaceæ, Clusiaceæ, Hypericaceæ, Quiinaceæ, Eucryphiaceæ, Ochnaceæ, Dipterocarpaceæ. Vestal (1937) found the anatomy of the woods to confirm as natural this generally accepted assemblage of families. They show nice transitions from primitive vessels with barred perforations to advanced vessels with porous perforations. Similarly in the flowers, there are transitions from spiral parts of indefinite numbers to whorled parts of definite numbers, while the endosperm varies from nuclear to cellular (Schnarf on *Saurauia*, 1924; Swamy on *Marcgravia*, 1948). The basic family Dilleniaceæ is

needed to bind together this assemblage; it might otherwise as well be included in Multisiliquæ.

Order 5. BICORNES L. Orders *Rhododendra* and *Ericæ* Jussieu Gen. Pl. 158, 159 (1789). Order *Ericales* Engler Syllab. 151 (1892). The vessel perforations vary in the Bicornes from barred to porous. The flowers are characteristically sympetalous (there are both primitive and derived examples with separate petals); the stamens are free of the corolla, with no ribbed endothecium (except in the primitive family Clethraceæ), the anthers opening through pores, the pollen grains united in tetrads. The endosperm is cellular: the first two divisions of the endosperm mother cell are transverse, producing a row of four cells, among which the terminal members give rise to haustoria. Nearly all authorities agree that this group is immediately related to *Saurauia*, which belongs in or next to Actinidiaceæ. The families are Clethraceæ, Ericaceæ, Empetraceæ, and Epacridaceæ. In many Epacridaceæ, the stamens are epipetalous and the anthers open through slits, and the pollen grains are solitary; but these plants are linked to Ericaceæ by clear lines of transition. The families Lennoaceæ and Diapensiaceæ, which have been placed in this order, do not belong to it, and are for the present left unplaced.

Order 6. GUIACANAE Jussieu Gen. Pl. 155 (1789). Order *Diospyrinæ* (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 37 (1864). Order *Ebenales* Engler Syllab. 155 (1892). Styracaceæ, Sapotaceæ, Symlocaceæ, Ebenaceæ, and other families. De Candolle condemned *tatonnement* (fumbling!) as a method of recognizing the natural system; yet it was the accident that I have *Styrax* in near-by foothills and a plant of *Camellia* in my back yard that enabled me to see that Styracaceæ is immediately related to Theaceæ.

Order 7. PASSIFLORINAE (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 50 (1864). Order *Rotaceæ* L., in part. Order *Cisti* Jussieu, the mere plural of a generic name. Order *Parietales* (Endlicher) Braun op. cit. 49. *Cistifloræ* Eichler. Vestal (1937) assembled the families Flacourtiaceæ, Bixaceæ, Cochlospermaceæ, and Cistaceæ as a natural group descended directly from Multisiliquæ. Whether the herbaceous families Passifloraceæ, Caricaceæ, Cucurbitaceæ, and Begoniaceæ, usually placed with these, belong with them or belong together, and whether Violaceæ and Resedaceæ belong with them, is apparently as yet uncertain.

Order 8. SENTICOSAE L. op. cit., the evident standard genus being *Rosa*. Orders *Papilionaceæ*, *Lomentaceæ*, and *Pomaceæ* L. Order *Rosifloræ* (Endlicher) Braun. Order *Rosales* Engler Syllab. 115 (1892). Tippo (1938) showed that Saxifragaceæ *sens. lat.*, Brunelliaceæ, Cunoniaceæ, and Rosaceæ belong together. Presumably Crassulaceæ, Pittosporaceæ, and Leguminosæ belong with them. They are derived directly from woody Multisiliquæ.

Order 9. RHOEADAE L., including orders *Corydales*, *Putamineæ*, and *Siliquosæ* L. Order *Rhoeadinæ* (Bartling as class) Braun. Order *Rhoeadales* Engler Syllab. 111 (1892). *Papaveraceæ*, *Tovariaceæ*, *Fumariaceæ*, *Capparidaceæ*, *Cruciferæ*; *Moringaceæ* and *Violaceæ* have been placed here. They are believed to be derived directly from *Multisiliquæ*.

To this point in this presentation, it is believed that the truth as to the main outline of the phylogeny of the dicots has been perceived. The order *Multisiliquæ* is primitive; *Julifloræ*, *Guttiferæ*, *Passiflorinæ*, *Senticosæ*, and *Rhoeadæ* are immediate derivatives; *Scabridæ*, *Bicornes*, and *Guaiacanæ* are secondary derivatives. A considerable number of further orders are recognizable, but their connections are less clear. Gundersen (1950) took note that most compound pistils with axile placentation pass during development through a stage in which the placentation is parietal. Considering this fact in connection with the principle that ontogeny recapitulates phylogeny, he thought it probable that the group here called *Passiflorinæ* is an important secondary center of variation, ancestral to most of the remaining dicots. It is arguable, on the contrary, that parietal placentation is not usually a primitive character, but a result of pædogenesis, that is, of courses of evolution by which the immature condition of a relatively primitive organism becomes the mature condition of its derivatives. Hallier (1905) would have derived many of the more advanced dicots from *Sterculiaceæ*. Purely as a speculation, it is here suggested that more orders than *Bicornes* and *Guaiacanæ* may be derived from *Guttiferæ*.

Order 10. PRECIAE L., including orders *Rotaceæ*, *Caryophyllei*, and *Holoraceæ* and *Succulentæ* L. in part. Orders *Curvembryæ*, *Centrospermæ*, *Polygonales*, *Opuntiales*, *Primulales*, and *Plumbaginales* of Engler and others. A matter of fifteen families, decidedly varied in gross characters. The bulk of the families are characterized by curved or coiled embryos. Schnarf (1931, 1933) found *Opuntiaceæ* definitely linked to these, perhaps in the neighborhood of *Aizoaceæ*, by embryological characters. The embryos are straight or nearly so in *Polygonaceæ* (in which the anatomy of the stem is anomalous, as it is also in *Amaranthaceæ* and *Chenopodiaceæ*), *Primulaceæ* (notably similar to *Caryophyllaceæ* in gross features) and *Plumbaginaceæ* (distinguished by embryological peculiarities).

In the middle of the Englerian system of the dicots, there is a long series of families, from *Pandaceæ* to *Cynomoriaceæ*, of which the majority are mere names to European and North American field botanists. Engler assembled many of these as two orders distinguished by the position of the ovules. In *Geraniales*, the ovule is epitropous, "turned up," either erect with the micropyle turned in or pendant with the micropyle turned out. In *Sapindales*, the ovule is apotropous, "turned down," either erect with the micropyle turned out or pendant with the micropyle turned in. The extensive study of woods principally of these families by Heimsch (1942) appears to have revealed a more natural grouping than the Englerian: the next three orders represent it.

Order 11. POLYGALINAE (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 36 (1864). Order *Polygalales* (Bessey as suborder, 1897) Hallier (1905). Wood with rays heterogeneous I or II A; parenchyma in apotracheal bands or scantily paratracheal; fiber-tracheids with conspicuously bordered pit-pairs. Humiriaceæ, Linaceæ, Erythroxylaceæ, Polygalaceæ, Krameriaceæ, Diclidantheraceæ, Trigonaceæ, Tremandræceæ, Zygophyllaceæ, Malpighiaceæ, Vochysiaceæ.

Order 12. TRIHILATAE L. Order *Terebinthinae* (Bartling) Braun. Order *Terebinthales* Wettstein. *Pinnatæ* Hutchinson. Rays heterogeneous II B or homogeneous; parenchyma banded or paratracheal; wood fibers with simple pits. Rutaceæ, Cneoraceæ, Simarubaceæ, Meliaceæ, Sapindaceæ, Hippocastanaceæ, Aceraceæ, Bretschneideraceæ, Connaraceæ, Burseraceæ, Terebinthaceæ. Julianiaceæ is to be reduced to Terebinthaceæ.

The action of botanical congresses in conserving numerous names of families was scarcely duly considered, since practically all of these names are valid by the letter of the code. As an exception, the name Terebint(h)aceæ (Jussieu as order) appears to have been applied definitely to a family before Anacardiaceæ was.

Order 13. GRUINALES L. Order *Geraniales* Engler. The wood (of woody examples) exhibits advanced characters, absence of scalariform perforations and presence of libriform fibers. Geraniaceæ, Oxalidaceæ, Tropæolaceæ, Balsaminaceæ. Limnanthaceæ, a small family of herbs of western North America, are in gross structure closely similar to Geraniaceæ. They are embryologically peculiar (having a 4- or 2-sporic embryo sac of unique type; Mason, 1951; Mathur, 1956), but may as well be placed here.

Order 14. TRICOCCEAE L. Euphorbiaceæ, an enormous family, chiefly tropical, grossly varied in every character as though not a natural group.

Order 15. COLUMNIFERAE L. Order *Malvales* Engler. Tiliaceæ, Malvaceæ, Bombacaceæ, Sterculiaceæ, and other families; a thoroughly natural group.

Order 16. CALYCANthemAE L. Orders *Calycifloræ* and *Hesperideæ* L., in part. Order *Myrifloræ* (Endlicher) Braun. Loasaceæ, Thymelæaceæ, Elæagnaceæ, Lythraceæ, Onagraceæ, Melastomaceæ, Myrtaceæ, and many others; needing further study.

Order 17. UMBELLATAE L. Order *Hederaceæ* L., in part. Order *Umbellifloræ* (Bartling as class) Braun. Cornaceæ, Araliaceæ, Umbelliferae. The suggestion that Garryaceæ also belongs here has been confirmed by a recent thorough study by Moseley and Beeks (1956).

Order 18. SANTALINAE Grisebach. Like Calycanthemae and Umbellatæ, these have choripetalous flowers with inferior ovaries; the characters may be obscured by reduction. Olacaceæ, Santalaceæ, Loranthaceæ, Balanophoraceæ, etc.

Among sympetalous dicots, the Bicornes, Guaiacanæ, and Primulales



have already been given places. As to the remainder, the evidence, particularly from the embryology, inclines one to treat them as a natural group of four orders, as follows.

Order 19. LURIDAE L., including orders *Campanaceæ* L. (Convolvulaceæ and Polemoniaceæ), *Personatæ* L. (Scrophulariaceæ, etc.), *Asperifoliæ* L. (Hydrophyllaceæ and Boraginaceæ) and *Verticillatæ* L. (Labiatæ). Order *Tubifloræ* (Bartling as class) Braun. About twenty-three families. In Bicornes and Guicacanæ, the cellular endosperm is inherited from certain Guttiferæ. In the present order it has evolved separately, the lower families, Convolvulaceæ and Polemoniaceæ, having nuclear endosperms. Whereas in Bicornes the endosperm mother cell undergoes two transverse divisions and produces a linear four-celled endosperm, in the present order it undergoes usually a transverse division followed by a longitudinal division, producing a T-shaped stage. The apetalous family Callitrichaceæ has the embryogeny of this group.

Order 20. CONTORTAE L., including *Sepiariæ* L. Seven families, a very natural group, apparently a minor offshoot of the preceding.

Order 21. STELLATAE L. Caprifoliaceæ and Rubiaceæ. The Adoxaceæ have the pollen of this group (Erdtmann, 1954).

Order 22. AGGREGATAE L. Eight families, including Campanulaceæ, Lobeliaceæ, Valerianaceæ, Dipsacaceæ, and Compositæ. In the Englerian system, part of these are in Rubiales, but the embryological characters (and, indeed, the characters in general) place them as here.

A large number of families remain unplaced. Places could be given to many of them by recognizing such orders as Juglandales, Aristolochiales, Sarraceniales, and Celastrales; but these are either small and themselves not certainly placed, or else not evidently natural. Surely, by sufficient study of anatomy, embryology, and palynology, we will eventually learn their true positions.

At the same meetings and on the same day on which this paper was given oral presentation, Dr. Arthur Cronquist presented a system of the dicots which is expected soon to reach publication. Cronquist places all of the families in orders, which, for the sake of definition by description, are made considerably smaller and more numerous than the ones here maintained. The orders are arranged in a phylogenetic pattern with which the one here presented is in essential agreement so far as it goes. The differences between his system and mine are as though we were artists representing the same tree under the conventions of different schools, and as though he had seen many more details than I (I have every reason to believe that he has perceived most of them correctly). The points of agreement allow us to believe that we are actually approaching the system of the future.

Sacramento Junior College,  
Sacramento, California

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## A BOTANICAL DISASTER

ERWIN F. LANGE

A chance meeting of two botanical explorers along the shores of the Columbia near The Dalles, Oregon, on November 13, 1843, left a story of disaster which completely altered the life of a German botanist, Frederick George Jacob Lueders. For on that day Lueders stood by helplessly as he watched the turbulent Columbia swallow up his entire botanical collection and collecting equipment. In a matter of seconds the results of three years' labor in the wild and mountainous parts of the United States were washed away. All that Lueders was able to rescue from the water was a treasured copy of his Torrey and Gray Flora.<sup>1</sup> This event would probably have gone unrecorded in the pages of Northwest science history had it not been for the famed United States explorer, Captain John C. Fremont, who witnessed the event and noted it in his journal. Concerning the calamity he wrote:

A gentleman named Lueders, a botanist from the city of Hamburg, arrived at the bay I have called by his name, while we were bringing up the boats. I was delighted to meet at such a place a man of kindred pursuits; but we had only the pleasure of a brief conversation, as his canoe, under the guidance of two Indians, was about to run the rapids; and I could not enjoy the satisfaction of regaling him with breakfast, which after his recent journey, would have been an extraordinary luxury.

All his few instruments and baggage were in the canoe, and he hurried around to meet it at Grave Yard Bay; but he was scarcely out of sight when, by the carelessness of the Indians, the boat was drawn into the midst of the rapids, and glanced down the river, bottom up, with a loss of everything it contained. In the natural concern I felt for his misfortune, I gave to the little cove the name of Lueders' Bay.

Fremont's note aroused but little interest until Leslie L. Haskins came to Brownsville, Oregon, as a photographer and botanist. As a small boy in

<sup>1</sup> This book is today a part of the library collection of the Oregon Historical Society. Augusta Lueders, a daughter of the German botanist, sent it to Leslie L. Haskins, author of "Wild Flowers of the Pacific Coast," who presented it to the Historical Society library.

Sauk City, Wisconsin, around 1890 he had often seen and heard of an old German gardener and botanist, Frederick G. J. Lueders, a resident of that community. On coming to Oregon, Haskins was surprised to find that no one could give him information regarding the life and activities of the German botanical explorer. Only as the result of an intensive correspondence was Haskins able to uncover the story of Lueders' life. The material was supplied by Miss Augusta Lueders, daughter of the botanist.

Frederick Lueders was born in Hamburg, Germany, on October 3, 1813, the son of a gardener. In Hamburg he attended a private school and later studied botany at the Hamburg Botanical Gardens. Then he entered the large seed house of Haage in Erfurth, Saxony. On returning to Hamburg, the Society for Natural Science offered Lueders the opportunity for scientific exploration in the United States. To qualify for the opportunity, Lueders again attended school to learn navigation, and at graduation he qualified for first mate.

Concerning the coming years of his life, Lueders wrote<sup>2</sup> a friend in 1861:

I arrived in Sauk Prairie in July, 1841, in company with my friend . . . We reached Green Bay by way of the lakes, and passed through the richly wooded country, which borders upon the Fox River and Lake Winnebago. Leaving the forest and entering the open country, we were much surprised at the beauty of the natural park. At that early time a few farms only guided the stage road. In almost every house where we stopped, the hospitable people invited us to spend a few days at their new home, and share what their humble plantation could afford, of course without pay. Arrived at Fort Winnebago, the terminous of the stage. The fortification was still garrisoned; there was besides a store, tavern and blacksmith's shop near the fortress. From there we went down the Wisconsin River by a boat of the French fur trader.

I spent the rest of the season about Sauk prairie in collecting several hundred species, in part, very interesting plants.

Although I did not intend to spend the winter there, I was surprised by it before I could find conveyance to the Mississippi.

In March, 1842, I went to Galena, And from there to St. Louis. There I found an easy introduction in my pursuit, as a Dr. Asa Gray, of New York, had kindly furnished me with a letter to Dr. Engelmann, whose services for the development of Western horticulture are amply known.

After a short stay in the city I proceeded to search the western part of Missouri, collecting plants and curiosities. On my excursion to that part of Missouri, I found opportunity to gather information about the Western country, and resolved to pursue the next spring a westerly course as far as terra firma would permit me to study and collect the flora of the mountainous country. In the meantime there had awakened a spirit of emigration to Oregon, and large bodies of emigrants were along the frontier of Missouri forming several companies. One of these I joined leaving the civilized world in May, 1843.

In the course of the journey, I collected plants and noted down peculiarities as circumstances would permit.

The loss of my baggage in the rapids below the Grand Cascades of the Columbia River, rests not only severe with the collection of plants, but perhaps more so with a good many valuable instruments and other collecting material, as I had fitted myself out to spend several years in that part of the country.

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<sup>2</sup> Letter in herbarium, University of Oregon, Eugene.

The kindest assistance was offered me by the gentlemanly officers of Fort Vancouver, but could not lead me into the course which my enthusiastic mind had marked out, and from there all communication by letter was tedious and uncertain. I concluded to return to Europe and engage anew, after having gained some useful experience.

In February, 1844, I left the mouth of the Columbia River for the Sandwich Islands, and proceeded from there to Chile, touching the Paradise of the Pacific (Otaheite), then in a state of siege. I arrived in Hamburg in November of the same year.

In the short space of my absence, family circumstances had taken a change, that made my presence there, at least for several years, necessary. So the course nearest my heart, for future life, was beyond my individual control.

At Christmas, 1844, I again hailed the Mississippi. I lived at St. Louis until 1851, and after that time in Sauk County (Wisconsin) tilling the soil and my mind.

— F. G. J. Lueders

He spent the rest of his life in Sauk City, Wisconsin, and engaged in many astronomical studies. In 1869 he had published in Hamburg "The Aurora Borealis and Law of Reciprocal Action in the Universe" and in 1884 the University of Wisconsin published his observations on a number of Auroras which he had studied. Privately, Lueders also published a pamphlet "Memoirs on Physical Astronomy." For many years he was city treasurer of Sauk City. He died December 21, 1904.

Thus a botanical disaster prevented Lueders' name from being associated with Northwest botany. Had his specimens been properly reported, there is no doubt that his name would have been linked with species of western plants. Lueders' Bay, named by Fremont, is also a lost geographical name. One can only speculate on its location, and as the large dams on the Columbia are changing the topography along the river, Lueders' Bay itself may no longer be in existence.

Portland State College,  
Portland, Oregon

### ROBERT HIBBS PEEBLES<sup>1</sup>

The death, last March, of Robert Hibbs Peebles, one of the world's leading cotton breeders and an outstanding student of cotton genetics, was a great loss to southwestern agriculture. He was the originator of what had become, in recent years, the preferred variety of Pima (American-Egyptian) long-staple cotton, and carried on investigations of the inheritance of various characters of this very important crop-plant. Toward the end of his career he was working on the problem of how to insure the greatest possible degree of natural cross-pollination, in view of the fact that artificial cross-pollination of cotton varieties usually increases the yield, as compared with that of either parent. The endeavor was to do, with cotton, what has been done so successfully with hybrid corn.

<sup>1</sup> This paper was in press at the time of Dr. Kearney's death on October 19, 1956.  
—Ed.



FIG. 1. Robert H. Peebles at his home, Sacaton, Arizona, Christmas Eve, 1944.

The University of Arizona, recognizing the great value of Peebles' contributions to the agriculture of the state, conferred upon him an honorary D. Sc., less than a year before his untimely death, at the age of 55. He was also given, posthumously, the United States Department of Agriculture's Superior Service award and medal.

To taxonomic botanists, Dr. Peebles was well-known as an ardent student of the native flora and co-author with me of "Flowering Plants and Ferns of Arizona" (1942) and "Arizona Flora" (1951). For two decades he devoted many of his week-ends to plant collecting in all parts of the state and added substantially to the number of species known to occur there.

He was especially interested in the Cactaceæ, which are such a conspicuous element of the Arizona flora, and he became a recognized authority on that family. The technique which he developed for preparing herbarium specimens of cacti has never been excelled. Some readers of this notice will recall his exhibition of specimens and photographs at a meeting of the California Botanical Society in April, 1953. His name is commemorated in that of the remarkable and very rare little cactus, *Navajoa Peeblesiana* Croizat.

The many friends of Bob Peebles will remember him always for his vivid and lovable personality. He was so very much alive that we can scarcely realize, even yet, that he is no longer with us. He has left a void that will be very hard to fill.—THOMAS H. KEARNEY, California Academy of Sciences, San Francisco.

## THE CHROMOSOMAL AND DISTRIBUTIONAL RELATIONSHIPS OF LUPINUS TEXENSIS AND L. SUBCARNOSUS (LEGUMINOSAE)

B. L. TURNER

The genus *Lupinus* is represented in Texas by several species (Shinners, 1953). Of these, the two most commonly encountered are *L. texensis* Hook. and *L. subcarnosus* Hook. The latter taxon is the official state flower of Texas, though *L. texensis* is sometimes mistaken for this species. Both species are endemic to the state and are known locally as bluebonnets. They are probably the most important native rangeland legumes in central Texas, often occupying hundreds of acres of rolling hillsides during the early spring months. The roots of these species are highly nodulated and are undoubtedly important soil nitrifiers. In addition, *L. texensis* has become a popular garden ornamental in many parts of the world. (Although many trade catalogues list *L. subcarnosus* as the Texas bluebonnet, most of the material on the open market appears to be *L. texensis*.)

### GEOGRAPHICAL DISTRIBUTION

*Lupinus texensis* occurs naturally on open calcareous soils throughout central Texas. *Lupinus subcarnosus* is restricted to sandy soils of south-central Texas. The interfingering distribution of the two species (Fig. 1) can be related to alternating grassland — forest strips which occur on deep clay and sandy soils respectively. The ecotone between these vegetative types is sharp, and consequently both species may be found growing in close proximity along many miles of the contact area. *Lupinus texensis* has a wide ecologic amplitude and may grow in a variety of disturbed soil types. As a result, the species has become established along road shoulders which cross the otherwise unoccupied sandy lands, particularly as a result of deliberate sowing by state highway workers and other wild-flower enthusiasts. *Lupinus subcarnosus* is rarely if at all sown along highways, and in no instance has the author seen the plant growing naturally on clay soils or along highways in such areas. In the numerous cases where both species were found growing together during the spring of 1955, no sign of morphologic intergradation, meiotic irregularity, or other evidence of hybridization could be detected.

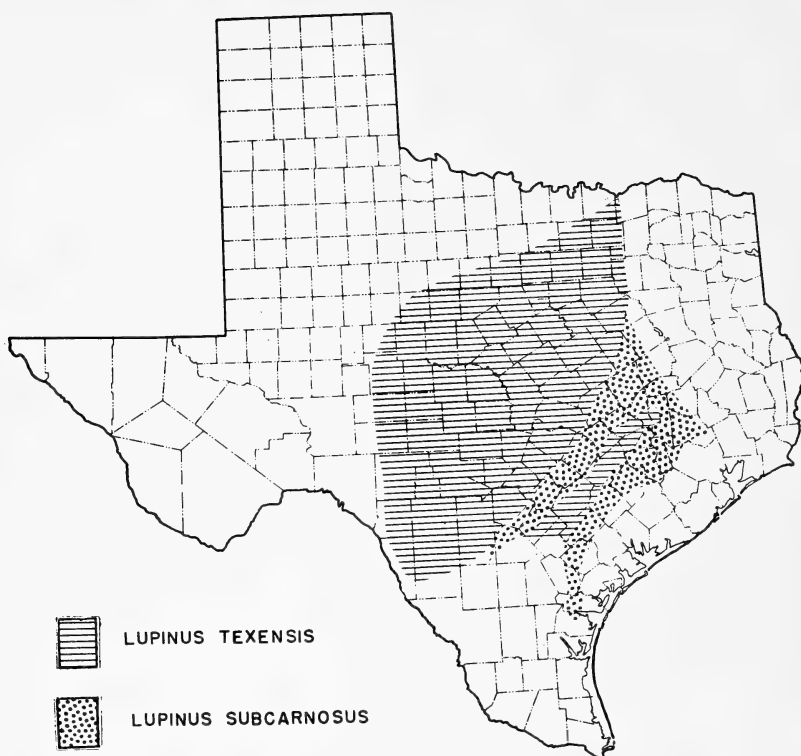


FIG. 1. Probable natural distribution of *Lupinus texensis* and *L. subcarnosus*. Based on herbarium records at The University of Texas and extensive field observation. Further explanation in text.

#### CHROMOSOME NUMBERS

Previous to the present study, two different counts had been reported for *L. subcarnosus*. Savchenko (1935) reported  $2n = 48$  and Tuschnjakowa (1935) reported  $2n = 36$  for this species. Because of the past confusion in the application of the names *L. texensis* and *L. subcarnosus* (Shinners, 1953), it was at first thought that the two differing counts might be for *both* species instead of *L. subcarnosus* alone. As a result, meiotic studies<sup>1</sup> of natural populations of these two taxa were undertaken. However, it was soon discovered that both *L. texensis* and *L. subcarnosus* had the same chromosome number of  $n = 18$ . In all instances, meiosis was completely regular, metaphase plates showing 18 bivalents and anaphase plates were without bridges. Counts obtained are given in Table 1.

<sup>1</sup> Buds were killed and fixed in a mixture of 4 chloroform:3 absolute alcohol:1 glacial acetic acid. Anthers were squashed in acetocarmine 2 to 3 days after collection. Voucher specimens are deposited at the University of Texas Herbarium, Austin, Texas.



TABLE 1. CHROMOSOME COUNTS OF LUPINUS SUBCARNOSUS AND L. TEXENSIS

Species	Collection	n number
<i>L. subcarnosus</i>	Bastrop County: Bastrop State Park. <i>Turner 3703.</i>	18
<i>L. subcarnosus</i>	Bastrop County: 4 miles west of Bastrop. <i>Turner 3704.</i>	18
<i>L. subcarnosus</i>	Gonzales County: near Palmetto State Park entrance. <i>Turner 3708.</i>	18
<i>L. subcarnosus</i>	Fayette County: 2 miles west of Moulton. <i>Turner 3712.</i>	18
<i>L. subcarnosus</i>	Lavaca County: Sublime. <i>Turner 3719.</i>	18
<i>L. subcarnosus</i>	Colorado County: 5 miles west of Altair. <i>Turner 3723.</i>	18
<i>L. subcarnosus</i>	Fort Bend County: 0.5 mile east of Fulshear. <i>Turner 3727.</i>	18
<i>L. subcarnosus</i>	Austin County: San Felipe State Park. <i>Turner 3730.</i>	18
<i>L. texensis</i>	Travis County: Austin. <i>Turner 3699.</i>	18
<i>L. texensis</i>	Lavaca County: 2 miles west of Moulton. <i>Turner 3713.</i>	18
<i>L. texensis</i>	Lavaca County: 1 mile southeast of Shiner. <i>Turner 3718.</i>	18
<i>L. texensis</i>	Austin County: 3 miles east of Ulm. <i>Turner 3732.</i>	18
<i>L. texensis</i>	Hays County: 10 miles west of San Marcos. <i>Turner 3733.</i>	18
<i>L. texensis</i>	Llano County: 3 miles northwest of Buchanan Dam. <i>Turner and Johnston 2523.</i>	18

Savchenko's number of  $2n = 48$  was apparently for some misnamed taxon, or else strains of *L. subcarnosus* and/or *L. texensis* exist in the ornamental trade as derived polyploids. Savchenko did not cite voucher material but merely indicated that the counts were made from seeds obtained from Germany.



FIGS. 2-3. Metaphase chromosomes of *Lupinus texensis* and *L. subcarnosus*: 2, *L. texensis*,  $n = 18$ ; 3, *L. subcarnosus*,  $n = 18$ . Camera lucida drawings,  $\times 2000$ .

## DISCUSSION

*Lupinus texensis* and *L. subcarnosus* are apparently very closely related as shown by their external morphological characters and their similar chromosome complements. However, they are clearly separated ecologically and in the field they are reproductively isolated. The reproductive isolation is perhaps partially due to the self-pollinating nature of the breeding populations; naturally occurring cross-pollinated individuals are probably rare. Experimental hybridization between these two species is being undertaken.

The discovery that both *L. texensis* and *L. subcarnosus* have chromosome numbers of  $n = 18$  has certain phyletic implications. Senn (1938), on the basis of Tuschnjakowa's reported number for *L. subcarnosus*, considered the species to be triploid in origin and thus, along with  $2n$  counts of 48 in other species, concluded the base number for the genus to be  $x = 12$  instead of 8, 9, 10, etc., as has been indicated by other workers (Darlington and Janaki-Ammal, 1945). Senn considered species with  $n$  numbers of 20, 21, 25, etc. to be derived aneuploids. The only other number of  $n = 18$  reported for the genus *Lupinus* is that made by Eickhorn (1949) on *L. tassilicus* Maire.

## SUMMARY

The distributional relationship of *L. texensis* and *L. subcarnosus* has been indicated. The former species is widespread throughout central Texas, occurring in calcareous soils; the latter is more restricted in range, occurring on sandy soils of south-central Texas. Meiotic counts from a number of localities in central Texas showed the chromosome number of both species to be  $n = 18$ . An earlier report of  $2n = 48$  for *L. subcarnosus* was probably erroneous. In spite of the morphological and chromosomal similarities of the two species, they do not hybridize in nature, even in habitats which permit their side-by-side occurrence.

The Plant Research Institute,  
University of Texas, Austin,  
and  
The Clayton Foundation for Research.

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# STUDIES ON THE CROSSABILITY OF LUPINUS TEXENSIS AND LUPINUS SUBCARNOSUS

LAWRENCE ERBE

During the period from March 17 to April 7, 1956, attempts were made to hybridize *Lupinus subcarnosus* with *L. texensis*. The work was begun just after *L. subcarnosus* began flowering. This was about two weeks later than *L. texensis* under the experimental conditions. The plants were most vigorous at this time as they had recovered from the shock of transplanting but had not yet started to decline in vigor. However, this vigorous condition could not be maintained. This factor doubtlessly was in part responsible for the low percentage of pods set from the various crosses and selfs. This is particularly true of the intraspecific crosses and selfings attempted on *L. texensis*, since these plants were the last to be worked upon and by that time they were no longer in optimum health.

The same emasculation and pollination techniques were employed as had previously proved successful on hybridization studies on the genus *Lotus* (Erbe, Master's Thesis, University of Vermont, 1955).

Stock plants of *L. subcarnosus* were obtained from a population occurring on sandy soil about ten miles west of Bastrop, Texas. Plants of *L. texensis* were obtained from a population occurring on the University of Texas campus in black clay.

On the basis of the present study, the tentative conclusion was that the two species are effectively isolated genetically. Certainly, they do not hybridize readily when subjected to experimental emasculation and pollination techniques. These experimental results as shown in Table 1 agree with the observation, presented by Turner (Madroño 14, p. 16), that there is no evidence of hybridization occurring when the two species grow sympatrically.

TABLE 1. RESULTS OF ATTEMPTED CROSSES IN LUPINUS

	No. of florets	No. of pods	Per cent of pods
Interspecific crosses:			
<i>L. texensis</i> × <i>L. subcarnosus</i>	52	0	0
<i>L. subcarnosus</i> × <i>L. texensis</i>	25	0	0
Intraspecific crosses:			
<i>L. subcarnosus</i> × <i>L. subcarnosus</i>	11	3	14
<i>L. texensis</i> × <i>L. texensis</i>	10	0	0
Selfed:			
<i>L. subcarnosus</i>	45	18	40
<i>L. texensis</i>	44	6	14

During the course of the study the writer bagged several inflorescences that were not used in the hybridization studies. Not a single floret of any of these inflorescences produced a pod. In addition, only one pod developed on the unbagged inflorescences of approximately fifteen other plants of *L. texensis*. Bee activity was almost non-existent; only one bee was

observed "working" an inflorescence. That particular inflorescence subsequently produced the only pod that developed on a *L. texensis* plant without experimental manipulation. It appears evident that pods are not produced by florets of *L. texensis* unless they have been "worked" by bees or man. Several of the unbagged inflorescences of *L. subcarnosus* set a few pods.

The Plant Research Institute,  
University of Texas, Austin,  
and  
The Clayton Foundation for Research.

## NEW NORTH AMERICAN ANDROPOGONS OF SUBGENUS AMPHILOPHIS AND A KEY TO THOSE SPECIES OCCURRING IN THE UNITED STATES<sup>1</sup>

FRANK W. GOULD

The Old and New World andropogons of the subgenus *Amphilophis* comprise a relatively distinct group, recognized as a separate genus by many systematists including O. Stapf, C. E. Hubbard, A. Camus, J. T. Henrard, and S. T. Blake. Both *Amphilophis* Nash and *Bothriochloa* Kuntze have been proposed as generic names for the species comprising this subgenus, with *Bothriochloa* (1891) antedating *Amphilophis* (1901). The name *Amphilophis* was first used by Trinius as a section name under *Andropogon*. Included in the section were a number of species belonging to *Vetiveria*, *Sorghastrum*, and *Sorghum*, as well as *Andropogon saccharoides* and its allies. Hackel, in his monograph (1889), took up *Amphilophis* as a subgenus name for the *A. saccharoides* group. *Bothriochloa* never has been officially published as a subgeneric name.

The *Amphilophis* andropogons are distinguished primarily on the basis of inflorescence characters. The pedicels, and at least the terminal rachis joints, have thickened margins and a medial groove or a broad thin membranous central area. The inflorescence characteristically is a leafless terminal panicle, with several to numerous racemose branches. In a few species there are as few as two or three branches per inflorescence.

The following new species and new name combinations are proposed in *Andropogon* rather than in *Bothriochloa* primarily to conform with the standard United States treatments of the genus (Hitchcock, 1951; Swallen, 1951; Gould, 1951; Gleason, 1952; Harrington, 1954). The Latin diagnoses have been kindly supplied by Dr. Lloyd Shinnery of Southern Methodist University. Mr. Jason R. Swallen of the United States National Museum has aided in clarifying the relationships of generic and subgeneric names. The writer is indebted to the curators of the herbaria of

<sup>1</sup> Technical Bulletin No. TA 2384, Texas Agricultural Experiment Station, College Station, Texas.

the following institutions for the loan of specimens during the course of study: University of Arizona (ARIZ), University of California (UC), University of Michigan (MICH), University of Texas (TEX), Southern Methodist University (SMU), and Smithsonian Institution (US). Specimens of the Tracy Herbarium, A. and M. College of Texas, are cited as (TRACY). Collections of the writer are indicated by number alone. Nursery grown plants were made available through the facilities and seed introduction program of the Texas Agricultural Experiment Station, and the Plant Introduction Section of the United States Agricultural Research Service.

***Andropogon springfieldii*** sp. nov. Perennis caespitosa 30–80 cm. alta; nodi dense barbati pilis patentibus 3–7 mm. longis; foliorum laminæ 2–3 (–5) mm. latæ glabræ vel hispidæ prope ligulam bicrinatæ; inflorescentia dense villosa pilis 5–10 mm. longis, ramosa ramis 2–8 in axi 1–4 cm. longo, inferioribus raro ramulosis; racheos segmenta et pedicelli subæquales sulcati marginibus crassulis villosis; spicula sessilis 6.0–7.3 mm. longa, gluma inferiore acuta vel bifidula infra mediam pilosa interdum supra mediam glanduloso-punctulata, lemmatis arista 20–26 mm. longa; spicula pedicellata sterilis angusta 5 mm. longa, pedicello 1–2 mm. longior; meiosis pollinis regularis; chromosomata somatica 120.

Tufted perennial with culms 30–80 cm. tall; culm nodes densely bearded with spreading hairs, these usually 3–7 mm. long; leaf blades 2–3, occasionally to 5 mm. broad, glabrous or sparsely pustulate-hispid on the axial surface and with tufts of hair on each side of the ligule; panicle densely white-villous, with 2–8 racemose branches, these infrequently rebranched; rachis joints and pedicels about equal, with thickened, densely villous margins and a broad thin membranous central area; hairs of the inflorescence 5–10 mm. long; sessile spikelets mostly 5.5–7.3 (–8.5) mm. long, the first glume acute or minutely bifid at the apex, hairy on the lower third or half of the dorsal surface, occasionally with a faint glandular pit or depression above the middle; awn of the lemma 20–26 mm. long; pedicelled spikelet sterile, narrow, averaging 4–5 mm. long and 1–2 mm. longer than the pedicel; pollen meiosis regular; chromosome number  $2n=120$ .

Type: From plant grown in nursery of Texas Agricultural Experiment Station, College Station, Texas, *F. W. Gould 6642* (type, TRACY; isotypes, US, UC, TEX, SMU, ARIZ). Original seed from near Scholle, Socorro County, New Mexico (*Wayne Springfield*, 20 August 1950).

Distribution: Western Texas, New Mexico, and northern Arizona; Argentina.

Specimens examined: UNITED STATES. TEXAS. Andrews County: Shafter Lake, *Tharp et al. 43024* (TEX). Brewster County: Alpine, *Bailey 29931* (TRACY); Chisos Mts., *Lundell 13286* (UC); Glass Mts., *Warnock W370* (TRACY) Culbertson County; southeast of Van Horn, *Davis et al. 90* (TRACY); Guadalupe Mts., *Lee 67* (TEX); base of El Capitan, *Tharp* and *Gimbredé 51-1543* (TRACY); Pine Spring, *Young* in 1916 (TEX). Dawson County: *Texas Soil Survey* in 1922

(TRACY). Jeff Davis County: 30 miles west of Fort Davis, *Reeves and Morrow G-165* (P.I. 216668) (TRACY); northern part of county, *Burnett 9* (TEX). Presidio County: *Taylor* in 1941 (TEX). NEW MEXICO. Chaves County: Roswell, *Hinckley* in 1936 (MICH). Lincoln County: Carrizozo, *Grassl 239* (MICH). Sierra County: Cuchillo, *Archer 416* (MICH). Socorro County: Scholle, seed collected by *Springfield* in 1950. Type collection from plants grown at College Station, Texas, *Gould 6642* (TRACY, US, UC, TEX, SMU, ARIZ). Valencia County: Paguete, *Weatherwax 2763* (TRACY). Without locality, *Wright 2103* (TRACY). ARIZONA. Coconino County: Havasupai Canyon, *Clover 7121* (MICH). ARGENTINA. Buenos Aires: west of Argerich, *Eyerdam et al. 23510* (UC).

This plant most commonly has been identified as *Andropogon barbinodis* Lag., from which it differs typically in the smaller habit, narrower blades, longer nodal hairs, panicles with fewer branches, shorter axis, and more densely white-villous pedicels and rachis joints, and the lower chromosome number.

The genetical relationship of this species with other taxa of the *Amphilophis* section is obscure. The short panicle axis, few panicle branches, large spikelets, and occasional pitted glume of the sessile spikelet suggest relationship with *Andropogon edwardsianus* Gould. The latter has deeply pitted glumes and the minimum chromosome number of the New World taxa,  $2n=60$ .

The dense villous pubescence of pedicels and rachis joints of *A. springfieldii* is not equalled in any other North American species of the *Amphilophis* section. It is, however, very similar to the condition characteristic of South American plants referable to *A. saccharoides* var. *erianthoides* Hack. The latter, undoubtedly specifically distinct from *A. saccharoides*, also has a chromosome number of  $2n=60$ . Both *A. saccharoides* var. *erianthoides* and *A. edwardsianus* are known to occur in Uruguay. *Andropogon springfieldii* is known to the writer from Argentina and undoubtedly also is present in Uruguay.

***Andropogon reevesii*** sp. nov. Perennis caespitosa 30–80 cm. alta geniculata demum ramosa; nodi glabri vel puberuli; folia glauca scabra firma; vagina glabra; ligula membranacea 2–4 mm. longa; lamina 2–4 mm. lata longe acuminata glabra vel supra parce pilosa; inflorescentia 6–8 cm. longa subflabellata sat pilosa ramis 6–9 subæqualibus 3–6 cm. longis simplicibus vel inferioribus ramulosis in axi 1.0–3.5 cm. longo; racheos segmenta et pedicelli  $\frac{1}{2}$ – $\frac{3}{4}$  spiculas sessiles æquantes cum sulca media membranacea marginis crassulos ciliatos æquante; spicula sessilis 4–5 mm. longa glauca late acuta, gluma inferiore plerumque infra mediam parce pilosa superne marginibus scabris vel puberulis non pertusa; lemmatis fertilis arista 12–15 mm. longa; spicula pedicellata sterilis angusta 3.0–4.5 mm. longa pedicello longior; meiosis pollinis regularis; chromosomata somatica 120.

Perennial bunchgrass; culms mostly 30–80 cm. tall, geniculate and freely branching below in age; culm nodes puberulent to glabrous; leaves glaucous, scabrous, very firm in texture; sheaths glabrous; ligule membranous, 2–4 mm. long; blades mostly 2–4 mm. broad, relatively narrow and stiff, tapering to a long-acuminate tip, glabrous or with a few scattered

hairs on the axial surface; panicles 6–8 mm. long, somewhat flabellate, moderately hairy, with an axis 1.0–3.5 cm. long and usually 6–9 branches, these unbranched or the lowermost simply rebranched; panicle branches mostly 3–6 cm. long, the uppermost about as long as the lower; rachis joints and pedicels  $\frac{1}{2}$  to  $\frac{3}{4}$  as long as the sessile spikelets, with a membranous medial groove about as wide as the thickened ciliate margins; sessile spikelets mostly 4–5 mm. long, glaucous, broadly acute at the apex, the first glume usually with a few coarse hairs below the middle and scabrous or minutely puberulent on the margins near the apex, pitless; awn of fertile lemma mostly 12–15 mm. long; pedicellate spikelets sterile, narrow, mostly 3.0–4.5 mm. long, longer than the supporting pedicels; pollen meiosis regular; chromosome number  $2n=120$ .

Type: Collected 2 August 1954 from plant grown in nursery of the Texas Agricultural Experiment Station, College Station, Texas, *F. W. Gould 6647* (type, TRACY; isotypes, US, UC, MICH, TEX). Original seed from Arteago, about 15 miles east of Saltillo, Coahuila, Mexico (*R. G. Reeves and Judd Morrow G-640*, altitude 6,000 feet, October 15, 1953, P. I. 216183).

Distribution: Known only from the Arteago collection.

This plant is similar to *Andropogon wrightii* Hack. in general aspect but also appears close to *A. saccharoides* Swartz. From the former it differs in the stiff blades, the smaller, more reduced pedicelled spikelets, the smaller, consistently non-pitted sessile spikelets, and in the uniformly regular pollen meiosis. From the latter it differs in the narrow stiff blades, and the inflorescence with a relatively short axis, few branches, and long terminal branches. *Andropogon reevesii* has a chromosome number of  $2n=120$ , while typical *A. saccharoides* has  $2n=60$  chromosomes. *Andropogon saccharoides* var. *longipaniculata* Gould has  $2n=120$  chromosomes but has a much larger and longer panicle, broader blades, and is a larger plant in general.

***Andropogon hybridus*** sp. nov. Perennis cæspitosa erecta 30–80 cm. alta; nodi glabri vel puberuli; foliorum vaginæ virides glaucæ glabræ; laminæ 2–4 (–5) mm. latæ plerumque basin versus parce cilitæ sæpe in ambitu parce pilosæ; panicula 6–11 cm. longa non dense pilosa ramis 3–8 simplicibus vel inferioribus ramulosis in axi 0.6–3.5 (–4.5) cm. longo; racheos segmenta et pedicelli subæquales sulcati marginibus crassulis pilosis pilis apicem versus 5–7 mm. longis basin versus multo brevioribus; spicula sessilis 4.5–6.5 longa aristis 18–25 mm. longis, gluma inferior nitida luteo-viridi apicem versus quinquenervosa supra mediam glanduloso-pertusa, infra mediam plerumque parce pilosa; spicula pedicellata diminuta sterilis 2.2–3.6 mm. longa pedicello brevior; meiosis pollinis regularis; chromosomata somatica 120.

Perennial, with strictly erect culms in small to medium sized clumps; culms 30–80 cm. tall, moderately branched and leafy above the base; culm nodes glabrous or minutely puberulent; leaf sheaths green or glaucous,

glabrous; blades mostly 2–4 rarely –5 mm. broad, usually sparsely ciliate with long hairs near the base, often with a few hairs on the surfaces; panicles hairy but not densely so, 6–11 cm. long, usually with 3–8 primary branches on an axis 0.6–3.5, occasionally –4.5 cm. long, the lower branches often simply rebranched; rachis joints and pedicels about equal, with a broad, membranous, often dark-colored, central groove and thickened hairy margins, the hairs mostly 5–7 mm. long near the apex and much shorter towards the base; sessile spikelet 4.5–6.5 mm. long, with an awn 18–25 mm. long; first glume of sessile spikelet shiny, yellowish-green, with usually five greenish nerves apparent on the upper half, with a moderately deep glandular pit above the middle, and usually with a few stiff hairs on the lower one-third or one-half of the back; pedicelled spikelets highly reduced, sterile, mostly 2.2–3.6 mm. long and shorter than the supporting pedicel; pollen meiosis regular; chromosome number  $2n=120$ .

Type: Texas, La Salle County, two miles east of Cotulla, *F. W. Gould* 6978, 10 November 1955 (type, TRACY; isotypes, US, UC, TEX, MICH, SMU, ARIZ). The dominant grass along a low flat graded roadside ditch in a mesquite area, growing with *Pappophorum bicolor* and weedy forbs in gravelly red-brown clay. Type and isotypes from one plant.

Distribution: South-central Texas to northeastern Mexico.

Specimens examined: TEXAS. Atascosa County: Jourdanton, 6223 (TRACY); Pleasanton, 6283 (TRACY). Bee County: 6.6 miles west of Beeville, 6051 (TRACY). Bexar County: San Antonio, *Higdon* in 1936 (TEX). Burnet County: Marble Falls, 5959 (TRACY). Cameron County: near San Benito, *Faulkner* 94 (TRACY). Dimmit County: Asherton, 6004 (TRACY). Gillespie County: 8 miles east of Fredericksburg, 5354 (TRACY); 11 miles east of Fredericksburg, 6487 (TRACY). Gonzales County: 8.5 miles south of Smiley, 6066 (TRACY); 8.5 miles south of Smiley, 6067 (TRACY). Guadalupe County: 19 miles west of Sequin, 6939 (TRACY). Kerr County: Kerrville, 6484 (TRACY). Kleberg County: 11 miles west of Kingsville, 6043 (TRACY); Kingsville, 6034 (TRACY). La Salle County: Cotulla, 6978 (TRACY). Live Oak County: George West, 6047 (TRACY); *Cummins* 12 (TRACY). Matagorda County: Palacios, *Richmon* 26 (TRACY). Maverick County: 10.5 miles south Quemando, 5997 (TRACY); Eagle Pass, 6473 (TRACY); west of La Pryor, near county line, 6475 (TRACY). Nueces County: western Nueces County, *Tharp* 47428 (TRACY). Real County: Camp Wood, 6952 (TRACY); Leaky, 6482 (TRACY). Travis County: 20 miles northwest of Oak Hill, 5961 (TRACY). Uvalde County: Uvalde, 6479 (TRACY); Uvalde 6226b (TRACY). Val Verde County: 30 miles west of Del Rio, *Rose* 71 (TRACY). Webb County: *Tharp* 5255 (TEX). MEXICO. COAHUILA. Sabinas, 6471.

This plant is intermediate between *Andropogon edwardsianus* Gould and *A. barbinodis* Lag. both in morphological characteristics and in chromosome number. From *A. edwardsianus* it differs in having broader blades, better developed upper culm leaves, more branched culms whose nodes often are puberulent, glume of sessile spikelet hairy below, panicle usually larger and more branched, and a  $2n$  chromosome number of 120 rather than 60. From *A. barbinodis* it differs typically in the shorter, more erect, less branched culms, glabrous or puberulent nodes, narrower leaf blades, smaller panicles with fewer branches, these often all unbranched, shorter pedicellate spikelets, less hairy glume of sessile spikelets, and fewer chromosomes. In relatively few areas do plants of *A. barbinodis* have all sessile



spikelets pitted while in *A. hybridus* the sessile spikelets consistently are pitted.

*Andropogon hybridus* characteristically is a plant of moderately disturbed habitats. It is most frequent along low roadsides and fence-rows, often forming dense stands. Throughout its range it is consistently associated with *A. barbinodis* and either *A. saccharoides* var. *torreyanus* or *A. saccharoides* var. *longipaniculata* <sup>US</sup>.

Inflorescences of plants assumed to be hybrids between *A. hybridus* ( $2n=120$ ) and *A. saccharoides* var. *longipaniculata* ( $2n=120$ ) have been collected at two Texas localities (Bee County, 6.6 miles west of Beeville, 6050a; Uvalde County, 1.5 miles north of Uvalde, 6226c). No indications of hybridization between *A. hybridus* and *A. saccharoides* var. *torreyanus* or *A. barbinodis* have been observed. It is very possible, however, that the first two taxa, with  $n=60$  and  $n=30$  chromosomes respectively, have produced fertile allopolyploids referable to *A. barbinodis* ( $n=90$ ).

*Andropogon hybridus* appears to have arisen from one or more hybrids between *A. edwardsianus* ( $n=30$ ) and *A. saccharoides* var. *torreyanus*. Hybridization, followed by doubling of chromosome number, could well have produced this fully fertile species. *Andropogon hybridus* seems almost certainly to be a relatively "young" species whose success is correlated with man's occupation and development of the region in which it occurs. Despite its present abundance along roads and railroad rights-of-way, the favorite collecting sites of taxonomists, this grass is poorly represented in herbaria. All but one of the collections studied and cited in this paper were made in the last 20 years. A complete search has not been made of the large herbaria for early collections, but these are certain to be few.

***Andropogon palmeri*** (Hack.) comb. nov. *Andropogon saccharoides* Swartz subsp. *leucopogon* var. *palmeri* Hack., in DC. Monogr. Phan. 6:496. 1889. *Amphilophis palmeri* Nash, Fl. N. Amer. 17: 126. 1912.

Type: Palmer 305 "Mexico ad Rio Blanco." 1886.

Specimens examined: Specimens from plants grown at College Station, Texas, from the following seed collections. MEXICO. DURANGO: between Torreon and Durango City, *Morrow* and *Merrill* G705 (P.I. 216186), between Zacatecas and Durango City, *Morrow* and *Merrill* G736 (P.I. 216196). Identification of this material was made by Jason R. Swallen of the United States National Museum.

*Andropogon palmeri* is similar to *A. barbinodis* in growth habit and inflorescence characteristics. It differs from this species primarily in having densely villous blades and sheaths. The first glume of the sessile spikelet may or may not be glandular-pitted. Although no accurate chromosome count has been obtained, it is most likely that this species has  $2n=180$  chromosomes, the same as *A. barbinodis*.

ANDROPOGON BARBINODIS Lag. var. ***perforatus*** (Trin.) comb. nov. *Andropogon perforatus* Trin. ex Fourn. Mex. Pl. 2: 59. 1886. *A. saccharoides* subsp. *leucopogon* var. *perforatus* Hack., in DC. Monogr. Phan. 6:496. 1889. *Amphilophis perforatus* Nash, in Small, Fl. Southeast U. S.

66. 1903. *Bothriochloa perforata* Herter, Rev. Sudamer. Bot. 6:135. 1940. Type: *Berlandier* 641 "Envir. de Mexique."

Distribution: South-central U. S. and Mexico, Argentina, and Uruguay.

Specimens examined: UNITED STATES. TEXAS. Aransas County: Rockport, *Cates* in 1946 (TRACY). Bee County: west of Beeville, 6049 (TRACY). Bell County: near Little River, *Wolff* 2260 (TRACY). Hidalgo County: 12 miles north of Edinburg, 6024 (TRACY). Blanco County: west of Johnson City, 5963 (TRACY). Bosque County: 12 miles northeast of Walnut Springs, *Shinners* 10420 (SMU). Brooks County: 19 miles north of San Manuel, 6029 (TRACY). Brown County: Brownwood, 5681 (TRACY). Brewster County: Chisos Mts., *Sperry* 396 (TRACY). Caldwell County: Luling, 6938 (TRACY). Dimmit County: north of Carrizo Springs, *McCully* 32 (TRACY). Edwards County: Texas Agr. Exp. Station, Substation 14, *Cory* 52473 (SMU, UC), *Sperry* in 1947 (TRACY). Gillespie County: Fredericksburg, 5965 (TRACY); east of Seguin, 6069, 6070 (TRACY). Guadalupe County: 19 miles west of Seguin, 6942 (TRACY). Hays County: Kyle, *Tharp* in 1920 (MICH). Llano County: Llano, *Wolff* 3047 (TRACY); south of Valley Spring, *Smathers* 14 (TRACY); Enchanted Rock, *Tharp* 7699 (TEX). Maverick County: 16 miles east of Eagle Pass, 6973a (TRACY). McCulloch County: Lohn, *Whitaker* 50-16 (TRACY). McLennan County: east Waco, *Smith* 306 (TEX). Mitchell County: northeast of Colorado City, *Pohl* 4987 (SMU). Motley County: west of Matador, *Duval* 52-102 (RF 556) (TRACY). Pecos County: Fort Stockton, *Cory* in 1924 (TRACY). Palo Pinto County: west of Mineral Springs, *Whitehouse* 19296 (MICH, SMU). Somervell County: north of Glen Rose, *Evans* in 1951 (TRACY). Tarrant County: *Ruth* 1065 (MICH). Uvalde County: Montell, 6951 (TRACY); Sabinal, 6945 (TRACY). Young County: Graham, *Reverchon* 3439 (SMU). ARIZONA. Cochise County: Douglas, *Gould* and *Haskell* 4548, in part (SMU). Pima County: Santa Rita Range Reserve, *Culley* 58 (ARIZ). MEXICO. CHIHUAHUA. Agua Caliente, *LeSueur mex* 051, in part (SMU, UC); between Camargo and Parral, *Reeves* and *Morrow* G-493 (P.I. 216165), in part (TRACY); north of Chihuahua City, *Reeves* and *Morrow* G-362 (P.I. 216157) (TRACY). COAHUILA. 40 km. west of El Oro, *Harvey* 1275, in part (MICH); 10 miles north of Mondora, *Reeves* and *Morrow* G-328 (P.I. 216121) (TRACY). DURANGO. North of Durango City, *Reeves* and *Morrow* G-524 (P.I. 216122) (TRACY); between Durango City and Torreon, *Morrow* and *Merrill* G-841 (P.I. 216096) (TRACY); between Durango City and Mazatlan, *Morrow* and *Merrill* G-789 (P.I. 216088) (TRACY); between Durango City and Parral, *Morrow* and *Merrill* G-760 (P.I. 216080) (TRACY); Ignacio Allende, *Gentry* 6917 (ARIZ). HIDALGO. Ixtaccihuatl, *Purpus* in 1905 (UC); Pachuca, *Purpus* 1631 (UC, MICH); north of Zimapan, 7023 (TRACY). MEXICO (or D. F.). "Envir. de Mexique," *Berlandier* 641, fragment from type (US). SAN LUIS POTOSI. Charcos, *Whiting* 525 (TEX, ARIZ, MICH). VERA CRUZ: "Region d' Orizaba," *Bourgeau* 2374 (US). ZACATECAS. Zacatecas, *Pringle* 1761 (UC, ARIZ).

The writer's concept of this taxon is based on examination of a panicle fragment from the type and the original description by Fournier. The fragment, consisting of three inflorescence branches, was obtained for the United States National Herbarium by Dr. A. S. Hitchcock in 1907. The type is in the Trinius Herbarium at Leningrad and unavailable for study.

The following is a critical description of the fragment in the United States National Herbarium: longest raceme 6 cm.; rachis and pedicels ciliate with relatively long hairs; first glume of sessile spikelets averaging 5.8 mm. long, relatively narrow, rather thickly beset below the middle with stiff hairs, with a single moderately sized glandular pit or depression (averaging 0.23 mm. in diameter) about 2 mm. from the tip; awn of

lemma averaging 26 mm. long; pedicelled spikelets averaging 3.8 mm. long, slightly longer than the supporting pedicels.

Fournier in the original description stated, "Culmo ramiso, . . . nodis barbatis; panícula flabellata e fasciculatis divergentibus composita, . . .".

The hybrid origin of *Andropogon barbinodis* with its high chromosome number has been previously hypothesized (Gould, 1953). It is believed that the factors for pitted spikelets, short inflorescence axis, and brittle rachis have been introduced into this taxon from *A. edwardsianus* or directly from the Old World *A. pertusus* complex.

The glume pit occurs in *A. barbinodis* in all possible gradations, from a faintly discernible glandular spot on one or two spikelets of the panicle to a large, deep pit on all sessile spikelets. From one or more centers, the pit character has become dispersed in *A. barbinodis* populations almost throughout the range of the species. In North America the pits are most consistently present in plants of central Texas and eastern Mexico. Glume pits have been observed in specimens from New Mexico, Arizona, and even southern Utah (Washington County, near Springdale, *M. E. Jones 6071*, near St. George, *Gould 1359*).

It is the intent of the writer to assign to *A. barbinodis* var. *perforatus* all plants of the species in which the sessile spikelets predominantly are pitted. This criterion is somewhat arbitrary as there is no distinct break in the pitted-spikelet series, but it does conform with the established concept of the "perforatus" entity.

Plants referable to *A. barbinodis* var. *perforatus* generally have been confused with those of *A. hybridus* and *A. edwardsianus*, the only New World species consistently having pitted sessile spikelets. The *A. barbinodis* plants are most readily distinguished from those of these species by the taller, stouter, more freely branched and less strictly erect culms, broader blades, larger panicles, larger pedicelled spikelets, and more densely hairy glume of the sessile spikelet.

**ANDROPOGON SACCHAROIDES Swartz var. *pulvinatus* var. nov.** Perennis caespitosa 70–130 cm. alta; nodi plerumque breviter barbati; folia glabra sæpe glauca, laminis 5–10 mm. latis; panícula exserta 8–16 cm. longa ramis 8–15 in axi 7–12 cm. longo, axillis atro- vel brunneo-pulvinatis; rami inferiores 2–5 cm. longi ramulosi in anthesis patentes demum contracti sed basi curvati; racheos segmenta et pedicelli pilosi pilis apicem versus 6–9 mm. longis, sulcata sulca media lata membranacea plerumque atrata; spicula sessilis 3–4 mm. longa lato-oblonga late acuta; spicula pedicellata 3 mm. longa pedicello plerumque brevior; chromosomata somatica 60.

Perennial bunchgrass; culms 70–130 cm. tall; culm nodes mostly short-bearded; leaves glabrous, often glaucous, the blades 5–10 mm. broad; panicle well exserted, 8–16 cm. long, with an axis mostly 7–12 cm. long and 8–15 primary branches; lower panicle branches 2–5 cm. long, mostly rebranched, spreading in anthesis but contracting in fruit, the bases re-

maining bowed-out; panicle branches with blackish or brownish, usually hairy pulvini in their axils; rachis joints nearly as long as the sessile spikelets, the latter overlapping for  $\frac{1}{2}$  or less of their length; rachis joints and pedicels hairy, the hairs 6–9 mm. long near the apex, shorter below; groove of pedicel broad, membranous, usually dark-colored; sessile spikelets typically 3–4 mm. long, broadly oblong, with a broadly acute apex; pedicellate spikelets about 3 mm. long, usually slightly shorter than the supporting pedicels; chromosome number  $2n=60$ .

Type: Mexico. Coahuila, Rancho Sierra Hermosa, 40 miles west of Monclava, *F. W. Gould 6467*, 25 June 1952 (type, TRACY; isotype UC). On rocky, brushy slopes, at 6,700 feet altitude.

Distribution and specimens examined: Known only from the type collection and from plants grown at College Station, Texas, from seed from the type collection.

This variety differs from *A. saccharoides* var. *torreyanus* in the taller culms, larger panicles, spreading or loosely contracted inflorescence branches with axillary pulvini, and more widely spaced spikelets. From *A. saccharoides* var. *longipaniculata* it is distinguished by the spreading or more loosely contracted inflorescence branches, the pulvini, the more widely spaced and blunter spikelets, and the chromosome number of  $2n=60$  rather than 120.

KEY TO THE NATIVE AND NATURALIZED SPECIES OF ANDROPOGON SUBGENUS AMPHILOPHIS IN THE UNITED STATES

I. All or some sessile spikelets pitless\*

Pedicelled spikelets about as large and broad as the sessile ones.

Sessile spikelets more than 5 mm. long. Native species . . . 7. *A. wrightii*

Sessile spikelets less than 5 mm. long. Introduced species.

Panicle axis shorter than the branches; sessile spikelets never pitted . . . . . 9. *A. ischaemum*

Panicle axis longer than the branches; sessile spikelets without pits or irregularly pitted . . . . . 11. *A. intermedius*

Pedicelled spikelets much narrower and usually shorter than the sessile ones.

Sessile spikelets 4.5–7.3 mm. long, awns 20–33 mm. long (18–20 in California *A. barbinodis*); spikelets pitless or both pitted and pitless on the same panicle.

Panicle axis less than 5 cm. long; panicle branches 2–8; rachis joints and pedicels densely white villous; culms slender, not over 1 meter tall and usually much shorter; leaf blades rarely over 4 mm. broad; pollen grains averaging 36–41 microns in diameter; chromosome number  $2n=120$

6. *A. springfieldii*

Panicle axis typically 5–15 cm. or more long; panicle branches typically numerous, rachis joints and pedicels villous but not densely so; culms typically stout, often over 1 meter tall; leaf blades, at least some, often 5–8 mm. broad.

Panicles of the larger culms 14–25 cm. long; culms very stout, stiffly erect, 1.2–2.5 meters tall, bluish glaucous below the nodes; culm nodes bearded with spreading hairs 3–6 mm. long; pollen averaging 39–40 microns in diameter; chromosome number,  $2n=120$  . . . 5. *A. altus*

\*Refers to circular glandular depression on outer (first) glume.

- Panicles mostly 7–13 cm. long; culms curving-erect, tending to become decumbent and much-branched below in age, mostly 0.7–1.1 meters tall, not bluish glaucous below the nodes; culm nodes bearded with appressed hairs less than 3 mm. long; pollen averaging 45–52 microns in diameter; chromosome number,  $2n=180$ .
- Sessile spikelets all or mostly pitless . . . 8a. *A. barbinodis* var. *barbinodis*
- Sessile spikelets mostly pitted . . . 8b. *A. barbinodis* var. *perforatus*
- Sessile spikelets less than 4.5 mm. long, awn of lemma less than 19 mm. long; spikelets never pitted.
- Awns absent or not more than 6 mm. long . . . 1. *A. exaristatus*
- Awns present, 8–18 mm. long.
- Panicles 5–9, occasionally –13 cm. long; glumes ovate, dull green and most commonly with a whitish waxy bloom; pollen averaging 34–37 microns in diameter; chromosome number,  $2n=60$  . . .
- 2a. *A. saccharoides* var. *torreyanus*
- Panicles of the larger culms 10–20 cm. long; glumes narrowly ovate, shiny green; pollen averaging 39–42 microns in diameter; chromosome number,  $2n=120$ ; southeastern and southern Texas to northern Mexico . . . 2b. *A. saccharoides* var. *longipaniculata*

## II. All sessile spikelets pitted

- Pedicelled spikelets about as large and broad as the sessile ones.
- Sessile spikelets more than 5 mm. long. Native species . . . 7. *A. wrightii*
- Sessile spikelets less than 5 mm. long. Introduced species.
- Panicle axis shorter than the lower branches . . . 10. *A. pertusus*
- Panicle axis longer than the lower branches . . . 11. *A. intermedius*
- Pedicelled spikelets much narrower and usually shorter than the sessile ones.
- Panicle axis less than 5 cm. long; primary panicle branches mostly 2–7, rarely more than 8; culm nodes glabrous or minutely pubescent.
- Upper culm nodes glabrous; primary panicle branches never rebranched; first glume of sessile spikelet 5.5–7.0 mm. long, glabrous on back, with a relatively large and deep glandular pit; leaves mostly in dense basal tuft, the culm leaves reduced; leaf blades rarely over 2 mm. broad; chromosome number  $2n=60$  . . . 3. *A. edwardsianus*
- Upper culm nodes glabrous or puberulent; lower 1 or 2 panicle branches frequently rebranched; first glume of sessile spikelet 4.5–5.7 mm. long, usually sparsely hispid on back near base; glume pit relatively small and shallow; culm leaves well developed; blades 2–5 mm. broad; chromosome number,  $2n=120$  . . . 4. *A. hybridus*
- Panicle axis typically 5–15 cm. or more long; panicle branches numerous.
- Panicles of the larger culms 14–25 cm. long; culms very stout, stiffly erect, 1.2–2.5 meters tall, bluish glaucous below the nodes; culm nodes bearded with spreading hairs 3–6 mm. long; panicle axis and branches often remaining “kinked” from compression in the sheath; pollen averaging 39–40 microns in diameter; chromosome number,  $2n=120$  . . . 5. *A. altus*
- Panicles mostly 7–13 cm. long; culms curving-erect, tending to become decumbent and much branched below in age, mostly 0.7–1.1 meters tall, not bluish-glaucous below the nodes; culm nodes bearded with appressed hairs less than 3 mm. long; panicle axis and branches not “kinked”; pollen averaging 45–52 microns in diameter; chromosome number,  $2n=180$  . . . 8b. *A. barbinodis* var. *perforatus*

1. *A. EXARISTATUS* (Nash) Hitchc., Biol. Soc. Wash. Proc. 41:163. 1928. *Andropogon saccharoides* var. *submuticus* Vasey ex Hack. in DC.,

Monogr. Phan. 6:495. 1889. Not *A. submuticus* Steud., 1854. *Amphilophis exaristatus* Nash in Small, Fl. Southeast. U. S. 65. 1903. *Bothriochloa exaristata* (Nash) Henr. Blumea 4:520. 1941.

Distribution: Along the Gulf Coast of Louisiana and Texas; coastal Brazil, Argentina.

2a. *A. SACCHAROIDES* Swartz var. *TORREYANUS* (Steud.) Hack. in DC., Monogr. Phan. 6:495. 1889. *Andropogon glaucus* Torr., Ann. Lyc. N. Y. 1:153. 1824. Not *A. glaucus* Retz., 1789. *Andropogon torreyanus* Steud., Nom. Bot. ed. 2. 1:93. 1840. Based on *A. glaucus* Torr. *Andropogon jamesii* Torr. in Marcy, Expl. Red River 302. 1853.

Distribution: Alabama, Missouri and Colorado to northern Mexico.

2b. *A. SACCHAROIDES* var. *LONGIPANICULATA* Gould, Field and Lab. 23(1):17–19. 1955.

Distribution: Southern and southeastern Texas to northeastern Mexico.

3. *A. EDWARDSIANUS* Gould, Field and Lab. 19:183–185. 1951.

Distribution: Edwards Plateau of central Texas; Argentina and Uruguay.

4. *A. HYBRIDUS* Gould, sp. nov.

Distribution: Southern Texas and northeastern Mexico.

5. *A. ALTUS* Hitchc. Contr. U. S. Nat. Herb. 17(3):308. 1913.

Distribution: Western Texas and southern New Mexico to west-central Mexico; Bolivia and Argentina.

6. *A. SPRINGFIELDII* Gould, sp. nov.

Distribution: Western Texas and New Mexico to northern Arizona; Argentina.

7. *A. WRIGHTII* Hack. Flora 68:139. 1885. *Amphilophis wrightii* (Hack.) Nash. *Bothriochloa wrightii* (Hack.) Henr., Blumea 4:520. 1941.

Distribution: New Mexico and northern Mexico.

8a. *A. BARBINODIS* Lag. [Gen. et Sp. Nov. 3. 1816] var. *BARBINODIS*. *Amphilophis barbinodis* (Lag.) Nash in Small, Fl. Southeast. U. S. 65. 1903. *Bothriochloa barbinodis* (Lag.) Herter, Sudamer. Bot. Rev. 6:135. 1940.

Distribution: Texas, southern Colorado, Utah, and California, south to Argentina.

8b. *A. BARBINODIS* Lag. var. *PERFORATUS* (Trin.) Gould, comb. nov.

Distribution: South-central U. S., Mexico, Argentina, and Uruguay.

9. *A. ISCHAEMUM* L. Sp. Pl. 1047. 1753. *Amphilophis ischaemum* (L.) Nash, N. Amer. Fl. 17:124. 1912. *Bothriochloa ischaemum* (L.) Keng. Contr. Biol. Lab. Sci. Soc. China Bot. Ser. 10:201. 1936.

Distribution: Widespread in tropical and temperate regions of Asia,

Africa and Europe. Established as a pasture and wayside grass in Texas and occasional elsewhere in the United States from pasture plantings.

10. *A. PERTUSUS* (L.) Willd., Sp. Pl. 4:922. 1806. *Amphilophis pertusa* (L.) Stapf. in Prain, Fl. Trop. Afr. 9:175. 1917. *Bothriochloa pertusa* (L.) A. Camus, Ann. Soc. Lyon n. ser. 76:164. 1931.

Distribution: Tropical and subtropical Asia, Africa, and Australia. Occasional in southern Texas as a seeded pasture grass.

11. *A. INTERMEDIUS* R. Br., Prodr. Fl. Nov. Holl. 202. 1810. *Amphilophis intermedia* (R. Br.) Stapf in Prain, Fl. Trop. Afr. 9:174. 1917. *Bothriochloa intermedia* (R. Br.) A. Camus, Ann. Soc. Linn. Lyon n. ser. 76:164. 1931.

Distribution: China, India, the Indo-Malay region and Australia. Introduced as a pasture grass in Texas.

#### SUMMARY

Three new species, one new variety, and two new name combinations are proposed in *Andropogon*, subgenus *Amphilophis*. A key is presented to the eight indigenous and three naturalized species of this subgenus occurring in the United States. A unique feature of the key is the prominent use of the glume pit character. Of the species included in the key, the glandular glume pit is consistently present in three, consistently absent in four, and of variable occurrence in five.

Department of Range and Forestry,  
Texas Agricultural Experiment Station and  
A. and M. College of Texas, College Station, Texas

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## CHROMOSOME NUMBERS IN LUPINUS

LYLE L. PHILLIPS

The genus *Lupinus*, a member of the sub-family Papilionoideæ of the Leguminosæ, is a group of world-wide distribution with population centers in western United States, Europe, and South America. The present cytological study was undertaken in conjunction with a taxonomic revision of the perennial lupines of North America (Phillips, 1955) in which sixteen species and sixteen infra-specific taxa are recognized. Chromosome numbers are listed below for twenty-six of these taxa.



FIGS. 1-5. *Lupinus* meiosis and mitosis: 1, *L. laxiflorus* var. *laxiflorus*,  $M_I$ ,  $n=24$ ; 2, *L. sulphureus* subsp. *sulphureus*, Diak.,  $n=24$ ; 3, *L. saxosus*, late Diak.,  $n=48$ ; 4, *L. humicola*,  $T_I$ ,  $n=24$ ; 5, *L. sericeus* subsp. *sericeus*, c-mitotic metaphase,  $n=24$ . The camera lucida drawings of the chromosomes were made at a magnification of 1940 and reduced to 970.

The chromosome number determinations were made either at diakinesis or metaphase I of microsporogenesis or metaphase of root mitosis. The meiotic material was fixed in Carnoy III (3 parts ethanol, 4 parts chloroform, and 1 part acetic acid) and smeared in aceto-carmin or propionocarmine. Root tips were treated in oxyquinoline according to Tjio and Levan (1950) and smeared in aceto-orcin. Pollen fertility analyses were made with cotton blue lacto-phenol.



The present study on the perennial lupines and several previous reports on the chromosome numbers of Old World species (Kawakami, 1930; Savchenko, 1936; Tuschnjakowa, 1935; and Maude, 1940) make it apparent that the basic number of the genus is 12. Diploid ( $n=12$ ) and tetraploid ( $n=24$ ) species as well as several taxa that deviate from the basic number ( $n=21, 25, 26$ ) are cited for Europe and Africa. Of the

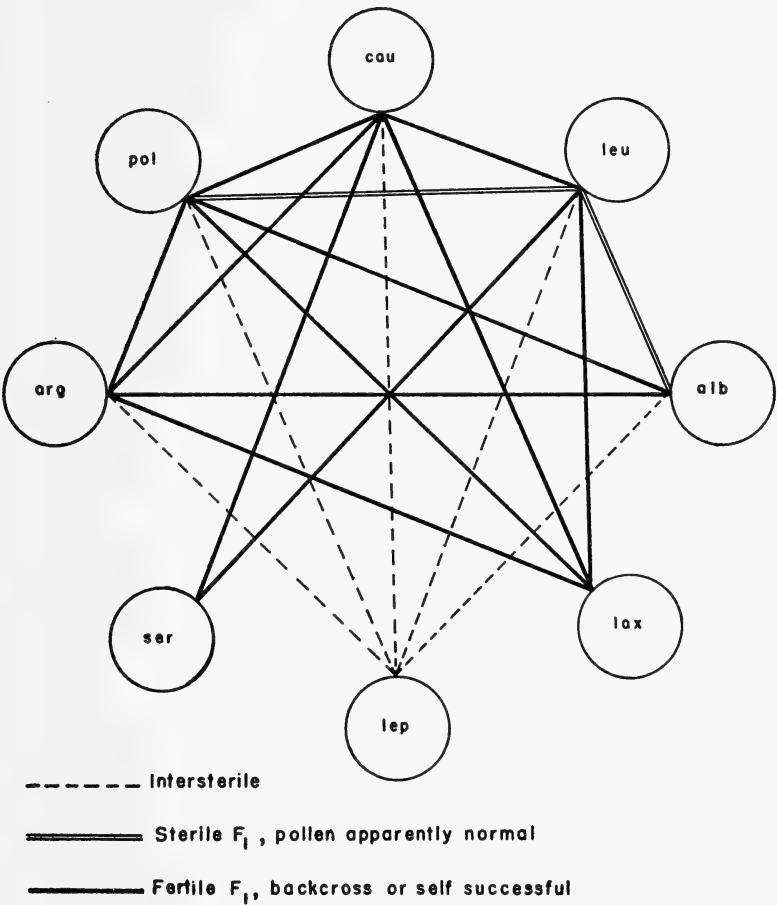


FIG. 6. Breeding behavior of eight species of *Lupinus* of the Northwestern United States. All taxa  $n=24$ : alb. = *L. albicaulis*; arg. = *L. argenteus* subsp. *argenteus*; cau. = *L. caudatus* subsp. *caudatus*; lax. = *L. laxiflorus* var. *laxiflorus*; lep. = *L. lepidus* subsp. *lepidus*; leu. = *L. leucophyllus*; pol. = *L. polyphyllus* var. *polyphyllus*; ser. = *L. sericeus* subsp. *sericeus*.

twenty-six North American taxa examined cytologically twenty are tetraploid, two are octaploid ( $n=48$ ), and four are both tetraploid and octaploid. The octaploid chromosome level has been heretofore unreported for the genus.

In none of the four taxa which contain two chromosome "races" is this difference in chromosome number correlated with morphological dissimilarities. Apparently the genetic isolation created by chromosome doubling in these taxa has not been operative long enough to permit divergence into morphologically definitive types. In a few instances populations of octaploids are somewhat unique as compared with related tetraploids, but these unique individuals or populations fall within the variation pattern of the taxon as a whole and cannot justifiably be given specific or infraspecific recognition.

Figure 6 presents a summary of a hybridization study involving eight tetraploid species native to Northwestern United States. It can be seen that all of the interspecific crosses were successful except those crosses involving *L. lepidus*. The  $F_1$  hybrids exhibited nearly regular meioses (occasionally lagging chromosomes were seen at metaphase I), and a fairly high degree of pollen fertility (75–85 per cent). Attempted crosses of *L. lepidus*  $\times$  *L. argenteus* and *L. lepidus*  $\times$  *L. leucophyllus* resulted in the production of normal seed pods containing aborted ovules. Since no such stimulatory effect on pod development was observed with other crosses involving *L. lepidus*, this is interpreted to mean that, of the species studied, *L. lepidus* is most closely related to *L. argenteus* and *L. leucophyllus*.

The apparent lack of genetic barriers between these species, demonstrable under experimental conditions, is also evident in the field where hybrid individuals often result wherever two or more species are sympatric. Occasionally hybrids and introgressants in such a sympatric association will completely blur species boundaries, but more often the discernible intermediates are relatively few in number. Presumably, the plants of hybrid nature are not able to compete with parental species except where there are uncolonized habitats available for which they are better adapted than the parents.

The low level of genetic differentiation between the species utilized in this study supplies a reasonable explanation for the extreme variability within species and for the overlapping variation pattern between many species. Species that can exchange genetic material readily are bound to be variable and difficult to separate taxonomically. Hence *Lupinus* has become known to taxonomists as a "difficult" genus.

For some of the wide-ranging taxa (*L. laxiflorus* var. *laxiflorus*, *L. sericeus* subsp. *sericeus*, *L. polyphyllus* var. *polyphyllus*) the citations listed below constitute only a portion of the collections counted. In these taxa the collections cited have been selected to reflect the geographical range from which cytological analysis has been made. The collections listed below are deposited in the Washington State College Herbarium.

TAXON	CHROMOSOME NUMBER (n)	COLLECTION
<i>L. albicaulis</i>	24	Seattle, King County, Washington, <i>Phillips</i> 690.
	24	5 miles south of Kelso, Cowlitz County, Washington, <i>Phillips</i> 667.
	24	Mollala, Clackamas County, Oregon, <i>Phillips</i> 720.
<i>L. argenteus</i>	24	5 miles west of Bridgeport, Baker County, Oregon, <i>Phillips</i> 634.
subsp. <i>argenteus</i>	24	Pierce, Clearwater County, Idaho, <i>Phillips</i> 786.
	24	Alberton, Missoula County, Montana, <i>Phillips</i> 860.
	24	10 miles east of Livingston, Park County, Montana, <i>Phillips</i> 855.
	24	12 miles west of Custer, Custer County, South Dakota, <i>Phillips</i> 846.
subsp. <i>parviflorus</i>	24	5 miles east of Soda Springs, Bear Lake County, Idaho, <i>Phillips</i> 792.
<i>L. caudatus</i>	24	Baker, Baker County, Oregon, <i>Phillips</i> 635.
subsp. <i>caudatus</i>	24	2 miles south of Madras, Jefferson County, Oregon, <i>Phillips</i> 627.
subsp. <i>argophyllus</i>	48	Monticello, Summit County, Utah, <i>J. Nishitani</i> 7-1952.
<i>L. humicola</i>	24	Leavenworth, Chelan County, Washington, <i>Phillips</i> 733.
	24	Near Manhattan, Broadwater County, Montana, <i>Phillips</i> 858.
	24	Acme, Sheridan County, Wyoming, <i>Phillips</i> 836.
<i>L. laxiflorus</i>	24	Omak, Okanagan County, Washington, <i>Phillips</i> 606.
var. <i>laxiflorus</i>	24	Winton, Chelan County, Washington, <i>Phillips</i> 728.
	24	Selah, Yakima County, Washington, <i>Phillips</i> 627.
	24	Near Mount Hood, Hood River County, Oregon, <i>Phillips</i> 621.
	24	6 miles east of Sisters, Deschutes County, Oregon, <i>Phillips</i> 707.
	24	2 miles south of White Bird, Idaho County, Idaho, <i>Phillips</i> 800.
	24	12 miles north of Boise, Ada County, Idaho, <i>Phillips</i> 803.
	48	Lyle, Klickitat County, Washington, <i>Phillips</i> 683.
	48	Underwood, Skamania County, Washington, <i>Phillips</i> 610.
var. <i>pseudoparviflorus</i>	24	Near Priest River, Bonner County, Idaho, <i>Phillips</i> 852.

TAXON	CHROMOSOME NUMBER (n)	COLLECTION
	24	St. Regis, Mineral County, Montana, <i>Phillips</i> 865.
<i>L. lepidus</i>	24	Spanaway, Pierce County, Washington, <i>Phillips</i> 582.
subsp. <i>lepidus</i>	24	3 miles south of Goldendale, Klickitat County, Washington, <i>Phillips</i> 612.
	24	Dayville, Grant County, Oregon, <i>Phillips</i> 630.
	24	Near Ukiah, Umatilla County, Oregon, <i>Phillips</i> 715.
	24	6 miles north of Modoc Point, Klamath County, Oregon, <i>Phillips</i> 892.
subsp. <i>lyallii</i>	24	Toll Gate, Umatilla County, Oregon, <i>Phillips</i> 699.
<i>L. leucophyllus</i>	24	Near Thorpe, Kittitas County, Washington, <i>Phillips</i> 642.
	24	2 miles north of Spangle, Spokane County, Washington, <i>Phillips</i> 876.
	24	Goldendale, Klickitat County, Washington, <i>Phillips</i> 658.
	24	Near Pullman, Whitman County, Washington, <i>Phillips</i> 842.
	24	La Grand, Umatilla County, Oregon, <i>Phillips</i> 636.
	24	Dixie, Baker County, Oregon, <i>Phillips</i> 633.
	24	5 miles north of Boise, Ada County, Idaho, <i>Phillips</i> 804.
	48	Near Goldendale, Klickitat County, Washington, <i>Phillips</i> 678.
	48	Wapato, Yakima County, Washington, <i>Phillips</i> 620.
<i>L. littoralis</i>	24	Hecata Beach, Lane County, Oregon, <i>Kruckeberg</i> 3315.
<i>L. polyphyllus</i>	24	Montsanto, Thurston County, Washington, <i>Phillips</i> 596.
var. <i>polyphyllus</i>	24	Mission Peak, Kittitas County, Washington, <i>Phillips</i> 676.
	24	2 miles east of Livingston, Park County, Montana, <i>Phillips</i> 851.
	24	Oswego, Clackamas County, Oregon, <i>Phillips</i> 646.
	24	Near Viola, Garfield County, Washington, <i>Phillips</i> 902.
var. <i>prunophilus</i>	24	Wawawai, Whitman County, Washington, <i>Phillips</i> 869.
<i>L. perennis</i>	24	4 miles east of Plymouth, Marshall County, Indiana, <i>Phillips</i> 822.
subsp. <i>perennis</i>		

TAXON	CHROMOSOME NUMBER (n)	COLLECTION
	24	Amboy, Lee County, Illinois, <i>Phillips</i> 815.
	24	Near Hanover, Lebanon County, Pennsylvania, <i>Phillips</i> 830.
subsp. <i>latifolius</i>	24	Mt. Rainier, Pierce County, Washington, <i>Phillips</i> 613.
	48	Zigzag, Clackamas County, Oregon, <i>Phillips</i> 628.
subsp. <i>plattensis</i>	24	5 miles east of Kimball, Kimball County, Nebraska, <i>Phillips</i> 809.
<i>L. saxosus</i>	48	10 miles south of Liberty, Kittitas County, Washington, <i>Phillips</i> 689.
<i>L. sericeus</i>	24	Maryhill, Klickitat County, Washington, <i>Phillips</i> 687.
subsp. <i>sericeus</i>	24	Big Timber, Sweetgrass County, Montana, <i>Phillips</i> 851.
	24	Gillette, Campbell County, Wyoming, <i>Phillips</i> 849.
	24	Orofino, Clearwater County, Idaho, <i>Phillips</i> 890.
subsp. <i>asotinensis</i>	24	Indian, Whitman County, Washington, <i>Phillips</i> 792.
	24	10 miles west of Clarkston, Asotin County, Washington, <i>Phillips</i> 811.
subsp. <i>sabinii</i>	24	Elgin, Union County, Oregon, <i>Phillips</i> 736.
<i>L. suksdorfii</i>	48	Glenwood, Klickitat County, Washington, <i>Phillips</i> 679.
<i>L. sulphureus</i>	24	Kooskooskie, Walla Walla County, Washington, <i>Phillips</i> 696.
subsp. <i>sulphureus</i>	24	2 miles east of Viola, Garfield County, Washington, <i>Phillips</i> 903.
subsp. <i>kincaidii</i>	24	Silverton, Polk County, Oregon, <i>Phillips</i> 721.
subsp. <i>subsaccatus</i>	24	10 miles south of Wenatchee, Kittitas County, Washington, <i>Phillips</i> 746.
	24	Cle Elum, Kittitas County, Washington, <i>Phillips</i> 688.
	48	Ellensburg, Kittitas County, Washington, <i>Phillips</i> 674.
	48	6 miles south of Coulee City, Grant County, Washington, <i>Phillips</i> 882.
subsp. <i>whithamii</i>	24	Butch Creek, Pend Oreille County, Washington, <i>Rumely &amp; Phillips</i> 453.
	24	Near Nordman, Bonner County, Idaho, <i>Rumely &amp; Phillips</i> 455.
	24	West shore of Priest Lake, Bonner County, Idaho, <i>Rumely &amp; Phillips</i> 456.

## SUMMARY

Chromosome number determinations for 26 taxa of North America indicate twenty of these to be tetraploid ( $n=24$ ), two to be octaploid ( $n=48$ ), and four taxa to be both tetraploid and octaploid.

A hybridization study involving eight species of Northwest United States shows genetic incompatibility barriers to be poorly developed between these species, thus supplying a possible reason for the overlapping patterns of morphological variation found in the genus *Lupinus*.

Department of Field Crops,  
North Carolina State College, Raleigh

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## JEROME D. LAUDERMILK

Mr. Jerome D. Laudermilk, who passed away in January, 1956, was a general scientist. The originality of his inquisitive mind impressed those who knew him well. He read widely and probed deeply as he read. Characteristically he was not satisfied to accept Leeuwenhoek's account of his microscope until he had ground lenses and made a microscope of his own exactly according to Leeuwenhoek's formula. The structure of ancient weapons was a special field of research, and he lectured and demonstrated his models publicly and for the Pomona College Department of Military Science and Tactics. He was interested so deeply in the operations of those who deal in the occult that at one time he was kidnapped, taken to an obscure house, and convinced that his life would be longer if he did not write on the subject.

Jerry Laudermilk was a graduate of Kansas State College of Pharmacy, and he served in the United States Army in World War I. Being in ill health he spent several years in the desert near Wickenburg, Arizona, where he developed a deep interest in and knowledge of desert vegetation. He came to southern California thirty-five years ago, and he lived for the last thirty years in Claremont, where he was Research Associate in Geochemistry and Paleobotany at Pomona College. There, in association with Dr. Philip A. Munz, he investigated the food habits of extinct giant sloths by study of the dung of the animals in the caves they inhabited in the deserts near the Colorado River. This has provided knowledge of the past vegetation of the area.

His interests carried him into many problems concerned with plants, minerals, fossils, and other natural objects. In his investigation of plants Mr. Laudermilk was never satisfied with the statements in books. He went directly to nature and drew or wrote from what he found there. He was an excellent illustrator of books and scientific papers and a painter of ability. He wrote many popular articles presenting science and especially botany and geology as a layman would enjoy it, and in these he brought knowledge from many fields to bear on matters commonly approached by a single avenue. His illustrations and manuscripts found their way into such journals as *Natural History*, *Desert Magazine*, and *Westways*. His last work was the principal series of illustrations for the writer's textbook entitled "Plant Classification," scheduled to be published in February, 1957. Mr. Laudermilk clung to life for many months in the hope of seeing these illustrations in print, and it is a great regret to the author that he was not able to do so.—LYMAN BENSON, Department of Botany, Pomona College, Claremont, California.

## ASTRAGALUS AGNICIDUS, A NEW LOCOWEED FROM HUMBOLDT COUNTY, CALIFORNIA

R. C. BARNEBY

The known history of the *Astragalus* described below goes back about twenty-five years, when Mr. Henry Tosten, the original discoverer, moved with his family to a ranch situated high in the outer North Coast Range near the divide between the South Fork of the Eel and the Mattole River in southern Humboldt County. Suffering great losses among his sheep, Mr. Tosten quickly identified this species as the culprit. In the summer of 1931 he prepared herbarium material and sent it to the late Mr. J. P. Tracy of Eureka, the outstanding authority on the flora of the region, and the specimens passed in due course to the University of California Herbarium at Berkeley, where I came across them in the winter of 1949. In May, 1954, I was able to visit the Tosten place and the genial owner obligingly took me up to the ridge above the ranch-house, the original station, where the locoweed still survived in sparing quantity. I am indebted to Mr. Tosten for the following information.

No sooner was the *Astragalus* recognized as poisonous than vigorous steps were taken to root it out. It was restricted to a wooded ridge, where the natural vegetation had been disturbed by logging, and was so abundant in early years that it was possible to collect great piles of stems for burning. Since then intermittent but never wholly successful attempts were made to control or exterminate it, and plans were afoot in 1954 to clear off the hilltop and plough it out. Mr. Tosten early assumed that the plant was an introduced weed; and it is said to be unknown to other ranchers in the community or county. A company of bark-strippers was

encamped on the site for some years before the Tosten occupancy, and this circumstance lends color to the view that it might have been brought in accidentally, possibly, as suggested by Mr. Tosten, from the Sacramento Valley. Yet it can be stated emphatically that it is not any species as yet recognized or described from the Americas. All attempts to identify the specimens with some Old World species having proved vain, I am forced to conclude that, in spite of its weedy occurrence, it is most probably native to California and requires a name.

The native status of *A. agnicidus* finds considerable support when we consider its probable relationships. It appears not to fit easily into any group described from Europe or Asia. On the typesheet Mr. Tracy remarked, in my opinion correctly, that it was near *A. umbraticus* Sheld., but differed in the pubescence and the pods. While *A. agnicidus* and *A. umbraticus* are readily distinguished at the specific level, as shown in the key below, they are much alike in general facies and organization, and together with *A. Congdoni* Wats. and *A. Paysonii* (Rydb.) Barneby form a small but homogeneous and presumably natural group in the genus. Leading technical characters common to the four species are: free stipules; thin-textured, often visibly penninerved leaflets; nodding or declined flowers and fruits; white petals; and pods shortly stipitate or subsessile, continuous with the receptacle (and hence falling naturally with the disjoining pedicels), in form obliquely linear- or lance-oblong, more or less incurved, compressed-triquetrous, grooved dorsally and fully bilocular. The three species known hitherto are all rare or highly localized. *Astragalus Congdoni* is endemic to the cismontane foothills of the Sierra Nevada, where it ranges in disjunct and scattered stations from the Mokelumne south to the Tule River, and is seemingly confined to areas of old metamorphic, sometimes partly serpentinized, bedrock. *Astragalus umbraticus* is known from only seven or eight stations, four of which lie in the Klamath Highland in southwest Oregon, on the Coquille, Rogue and Illinois rivers; from there it extends south to the lower Trinity River and Redwood Creek in Humboldt County, California; and it was collected long ago at an unspecified locality in the Coast Ranges of Yamhill County in northwest Oregon. The somewhat less closely related *A. Paysonii* is known as yet only from two records, one from the Snake-Green River divide in western Wyoming, the other at a point over three hundred miles distant to the northwest in the Clearwater Mountains of central Idaho. The distributional pattern of these species, considered individually and collectively, suggests that the section is a relatively old one, very likely composed of homogenic depleted species as defined by Stebbins (in *Madroño* 6:241-258, 1942). Stebbins has pointed out the alternative consequences of a change in environment on rare or relic species consisting of few biotypes: eventual extinction where the change is detrimental to their welfare, or regained vitality when conditions are altered to their advantage, or where competition is, even temporarily, reduced. It seems possible that disturbance of the highly competitive climax



woodland and the sudden weedy abundance of *A. agnicidus* are related phenomena. Further exploration of the more inaccessible parts of the North Coast Range may yet provide a definite answer.

The species discussed above may be distinguished by the following key:

1. Leaflets (except in a few early leaves) 15–35; flowers relatively large, the banner 9–16.5 mm., the keel 7–12.5 mm. long; cismontane Oregon and California.
2. Stems and herbage nearly glabrous, the few scattered hairs strictly appressed and not over 0.6 mm. long; ovary and pod glabrous; Coast Ranges, from Yamhill County, Oregon to central Humboldt County, California. Stipe of the pod 0.8–1.9 mm. long, the body 1.4–2.4 cm. long, 2.6–3.6 mm. in diameter, 10–15-ovulate ..... *A. umbraticus*
2. Stems (at least above the base) and herbage villous or pilose, the longest hairs at least 0.9 mm. long; ovary and pod pubescent; southern Humboldt County and Sierra Nevada, California.
3. Raceme compact and dense, the axis little-elongating, 2–4.5 cm. long in fruit; calyx-teeth linear or lance-acuminate, 3.3–5 mm. long; pod thinly villous-pilose, the stipe 0.3–0.4 mm., the body 11–15 mm. long, 3–3.4 mm. in diameter, 8–9-ovulate; Humboldt County..... *A. agnicidus*
3. Raceme open, becoming loosely secund and mostly 5–20 cm. long in fruit; calyx-teeth subulate, 1–2.5 mm. long; pod more densely strigulose-villosulous, the stipe 1–2.5 mm., the body (1.5) 2–3.5 cm. long, 2.3–3.2 mm. in diameter, 23–29-ovulate; Sierra foothills..... *A. Congdoni*
1. Leaflets 7–15; flowers small, the banner about 7 mm., the keel about 5 mm. long; western Wyoming and central Idaho. Stipe of the pod 1–1.5 mm., the body 10–17 mm. long, 2.5–3.5 mm. in diameter, 8–10-ovulate..... *A. Paysonii*

***Astragalus agnicidus* sp. nov.** Herbae elatae foliosae e radice verticali ramosa perenni, pilis debilibus patulis subsinuosis rectisque parce villosae, foliolis bicoloribus inferne pallidis ad nervum medianum barbatis, superne saturatius viridibus glabris, ciliatis, inflorescentia nigro-villosula; caules erecti et adscendentes fistulosi striati straminei (3) 4–9 dm. longi, ad medium ramosi vel subsimplices; stipulae membranaceae 4–15 mm. longae, imae ovato-triangulares amplexicaules inter se liberae, superiores lanceolato-acuminatae vel lineari-caudatae dimidium caulem amplectentes decurrentes deflexae; folia (3.5) 5–12 (16) cm. longa, superiora subsessilia, foliolis (6) 9–13-jugis petiolulatis ovato-vel lanceolato-oblongis obtusis vel emarginatis rarius acutiusculis mucronulatis (3) 5–22 mm. longis, majoribus penninerviis; pedunculi saepius 8–12 supra medium caulem emissi 5–13 cm. longi, folio subaequilongi; racemi dense (10) 15–40-flori, floribus mox patulo-declinatis, axi fructifero vix elongato (1) 2–4.5 cm. longo; bractee hyalinae lanceolatae vel lineari-caudatae 2–6 mm. longae reflexae; bracteolae minutae vel 0; calycis nigro-villosuli tubus campanulatus pallide membranaceus 3.2–4.2 mm. longus, 2.4–3 mm. latus, dentes firmiores virides lineares vel lineari-acuminati 3.3–4.9 mm. longi; petala alba immaculata; vexillum per 45° recurvum, oblanceolato-subrhombicum emarginatum, 9.1–11 mm. longum; alae 8.3–9.2 mm. longae, laminis oblanceolatis obtusis vel oblique obovatis emarginatis subrectis 5.4–6.5 mm. longis, 1.5–2.6 mm. latis; carina 7–7.4 mm. longa, laminis semi-obovatis 3.9–4.2 mm. longis, 2–2.4 mm. latis, per 90–95° in apicem obtusum deltoideum incurvis; legumen

patulo-declinatum subsessile, stipite vix 0.4 mm. longo calyce persistenti occultato, de visu laterali anguste lanceolatum paullo incurvum 11–15 mm. longum, 3–3.4 mm. latum, basi obtusum, apice in rostrum anguste triangulari-acuminatum cuspidatum angustatum, triquetro-compressum, sutura ventrali prominula concave arcuata carinatum, dorso anguste sulcatum, valvulis tenuibus piloso-villosulis demum chartaceis reticulatis stramineis, late inflexis, septo completo 1.5–2.2 mm. lato; ovula 8–9; semina (vix matura) brunnea laevia 1.7–2.1 mm. longa.

*Astragalo umbratico* Sheld. affinis, sed caulibus elatis, pube magis copiosa patula villosa multo longiori, dentibus calycinis elongatis, necnon legumine breviori villosulo 8–9 (nec 10–15)-ovulato summopere distincta.

The species name *agnicidus* is derived from *agnus*, lamb, and *caedere*, to kill; the species was first brought to notice by its reputedly poisonous qualities.

Specimens examined. CALIFORNIA. "Local on Tosten & Peirce Ranch, near Bear Buttes, 4 miles s. of Miranda, Humboldt County, alt. about 2500 ft., June 7, 1931, *Henry Tosten* ex herb. *J. P. Tracy*. Said to be a sheep poison and attempted to be eradicated, fall of 1931" (type, UC, two sheets, 502991, 502992). Topotypes: August 20, 1931, *J. C. Taris Jr.*, UC; May 19, 1954, just coming into flower, on brushy logged-over ridge, *Barneby 11570* (CAS, RSA, author's coll.).

Loan of the material at the Herbarium of the University of California, above cited, is hereby gratefully acknowledged.

Wappingers Falls, New York.

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#### NOTES AND NEWS

**ANEMOPSIS CALIFORNICA IN OREGON.** An apparently well-established clump of *Anemopsis californica* was found in an roadside irrigation ditch, along Crystal Springs Road about one mile southwest of the bridge that crosses Lost River, Klamath Falls, Oregon, on August 15, 1955 (*Pengelly 743*). The plant was associated with cattails (*Typha*) and arrow-leaf (*Sagittaria*); however, the ditch passes through typical *Artemisia tridentata* association. This appears to be the first record of the occurrence of this species in Oregon, the nearest known locality to the south being near the mouth of the Sacramento River.—RUSSELL PENGELLY, Klamath Falls, Oregon.

Some publications of interest follow:

*Responses of Vegetation to Fire*, by James R. Sweeney. University of California Publications in Botany 28 (4): 143–250, pls. 12–27, 10 figs. in text. 1956. \$2.00. University of California Press, Berkeley 4, California. A study of the effects of chaparral fires upon herbaceous vegetation.

*The Genus Clarkia*, by Harlan Lewis and Margaret Ensign Lewis. University of California Publications in Botany 20 (4): 241–392, 28 figs. in text. 1955. \$2.00. University of California Press, Berkeley 4, California. A monograph of the genus based upon a many-faceted, biosystematic approach to the problem.

*Variation and Genetic Relationships in the Whitlavia and Gymnobythus Phacelias*, by George Willson Gillett. University of California Publications in Botany 28 (2): 19–78, pls. 3–5, 16 figs. in text. 1955. \$1.00. University of California Press, Berkeley 4, California. A genetic analysis and systematic treatment of two of the seven subgenera of the genus *Phacelia*.

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# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 2

APRIL, 1957

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PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

# MADRÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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NOTES ON PACIFIC MARINE ALGAE<sup>1</sup>

PAUL C. SILVA

For the past ten years I have been engaged in taxonomic and phytogeographic studies of the marine algae of the Pacific coast of North America. Although it is planned to present the results ultimately as a floristic treatise, the completion of this project is so far from sight as to suggest the usefulness of publishing certain nomenclatural, taxonomic, and distributional notes at this time. All specimens cited in this paper are in the Herbarium of the University of California, Berkeley. Collections are mine unless otherwise indicated.

**Rosenvingiella** nom. nov. *Gayella* Rosenvinge (1893, p. 936). Non *Gayella* Pierre (1890, p. 26). Lectotype: *G. polyrhiza* Rosenvinge.

Although unanimity of opinion regarding the validity of this genus of Prasiolaceae is lacking, many phycologists prefer to regard the terete members of this family as constituting a genus separate from *Prasiola*. Unfortunately, the name *Gayella* had been used previously (in the Sapotaceae) by Pierre. Therefore I have proposed the substitute name, *Rosenvingiella*. Two species have been reported from the Pacific coast of North America.

**Rosenvingiella polyrhiza** (Rosenvinge) comb. nov. *Gayella polyrhiza* Rosenvinge (1893, p. 937, figs. 45, 46).

**Rosenvingiella constricta** (Setchell et Gardner) comb. nov. *Gayella constricta* Setchell et Gardner in Gardner (1917, p. 384, pl. 33, figs. 5-9; pl. 32, fig. 5).

*Rosenvingiella constricta* and *Prasiola meridionalis* Setchell et Gardner (1920) occupy a unique ecological niche: they are restricted to rocks (usually offshore) covered with guano and pounded by heavy surf, upon which they form patches or distinct bands in the spray zone. *Rosenvingiella constricta* inhabits only the lower part of this association, where it may grow intermixed with *Prasiola meridionalis* or in nearly a pure stand. The green patches or bands may be seen from a considerable distance, but only occasionally is one able to get close enough to discern the two component growths, which differ slightly in color. Still more rarely is one able to collect from these rocks, so that the range of these associated species as indicated by documented records probably is smaller than the actual range. Heretofore these two species have not been recorded south of Carmel Bay. Although I have observed probable stands along the central California coast south of Carmel and on the Channel Islands, only once did circumstances permit collections to be made (Forneys Cove, Santa Cruz Island, 12 March 1950).

<sup>1</sup> Grateful acknowledgment is made to the National Science Foundation and to the Research Board of the University of Illinois for grants in support of this study.

**Ectocarpus dimorphus** nom. nov. *Ectocarpus variabilis* (Saunders) G. M. Smith (1942, p. 647, figs. 1-4).

This distinctive species is commonly found growing on various Laminariales. Since *E. variabilis* G. M. Smith is a later homonym of *E. variabilis* Vickers (1905, p. 59) from Barbados, and since no other epithet is available, I have proposed a name which refers to the two kinds of plurilocular organs found in this species.

**DICTYOPTERIS JOHNSTONEI** Gardner (1940, p. 270, pl. 35). This species, which was published posthumously, is based on a "single, apparently fragmentary, part of a plant" dredged from 25 fathoms at Lone Cove, Santa Cruz Island, California (*G. R. Johnstone* 96, 28 November 1928, UC 472507). It is supposedly distinguished from *D. zonarioides* Farlow (1899) by the narrow segments and inconspicuous midrib. Hollenberg (1948) reported this species from "a large tide pool at medium high tide level on exposed rocky shore several miles south of Redondo Beach." Hollenberg's plant differs from the type, however, in being larger, coarser, and with well-developed percurrent axes. Material agreeing with the type was dredged by an Allan Hancock Foundation Expedition (Station 1431-41, 26 September 1941) off White Cove, Santa Catalina Island (Dawson, 1949, p. 21). Abundant material of *Dictyopteris* was dredged from 40 meters at the same locality by the M/V *Orca* of the J. W. Sefton Foundation Expeditions (4231, 8 February 1949), providing a series of specimens that strongly suggests the conspecificity of *D. johnstonei* and *D. zonarioides*. Although many specimens are typical *D. zonarioides*, others show a diversity of segment size, having some branches typical of *D. zonarioides*, other branches typical of *D. johnstonei*, and still other branches intermediate. Entire plants of the narrow *D. johnstonei* form were collected on the north shore of the west island, Islas San Benito, Baja California, Mexico (6409, 4 February 1950). The significance of this form remains to be demonstrated.

**Laminaria setchellii** nom. nov. *Hafgygia andersonii* Areschoug (1883, p. 3). *Laminaria andersonii* (Areschoug) Farlow ex Anderson (1891, p. 220). Non *L. andersonii* Eaton ex Hervey (1881, p. 98).

The name *Laminaria andersonii* has been applied to two species, and unfortunately the earlier application was to the species currently called *L. sinclairii* rather than to the plant which has been assumed to be *L. andersonii*. Doty (1947, p. 40) remarked that from Hervey's description of the blade "one would be inclined to think that he was referring to *L. Sinclairii*." However, from Hervey's statements that the plant grew on rocks with *Pterygophora* and that it had "the usual branching hold-fast" Doty concluded that *L. andersonii* as usually interpreted was definitely indicated. Hervey described a specimen (which unfortunately I have not been able to locate) sent by Dr. C. L. Anderson from Santa Cruz, California, with a stipe one-sixth of an inch thick and about eighteen inches long bearing a blade about an inch wide and eighteen inches long. This descrip-



tion clearly refers to *L. sinclairii*. Indeed, on the label of specimen no. 118 of Farlow, Anderson and Eaton's Algae Exsiccatae Americae Borealis, "*Laminaria Andersonii* Eaton mscr in Rep't. U.S. Fish Comm. 1875," is listed as a synonym of *L. sinclairii*. Further clarification is provided by Farlow (1881): "Since it was ascertained that the species called *L. Andersonii* was the same as *Lessonia Sinclairii* the manuscript name of *L. Andersonii* has been applied by Prof. Eaton and myself to a second species from the California coast which belongs to the digitate division of the genus and not to the section *Saccharinae*." Hervey apparently was not aware that the plant to which the manuscript name *L. andersonii* was originally applied has been recognized as *L. sinclairii*, and he thus unwittingly created a nomenclatural problem by effecting valid publication.

The epithet *andersonii* in its revised application was not validated until 1883, when Areschoug published it under *Hafgygia*. It was transferred to *Laminaria* by Anderson (1891), but the resulting combination is a later homonym and hence illegitimate. Inasmuch as no legitimate epithets are available for this species, I have proposed a new name in honor of W. A. Setchell, one of the foremost contributors to our knowledge of the Laminariales.

Heretofore the known range of this species has been Whidbey Island, Washington, to Carmel Highlands, Monterey County, California (Smith, 1944, p. 137). There are no herbarium specimens to authenticate the statement of Setchell and Gardner (1925, p. 605) that this species occurs as far north as Sitka, Alaska. The following collections extend the range northwest to Vancouver Island, British Columbia, and south to Santa Barbara County, California, and to certain of the Channel Islands.

CANADA. BRITISH COLUMBIA. Vancouver Island: Point No Point, 16 miles west of Sooke, 7056. UNITED STATES. CALIFORNIA. Monterey County: mouth of Malpaso Creek, 3622; Kasler Point, 814; Point Sur, 1101; Partington Point, 2256; Lucia, 2844. San Luis Obispo County: Point Piedras Blancas, 1359; Cayucos, 2317. Santa Barbara County: Point Sal, 5136; Point Pedernales, 2402; Point Arguello, 2541; Point Conception, 2468. San Miguel Island: Cuyler Harbor, 3743. Santa Rosa Island: Sandy Point, 4128. Santa Cruz Island: Fraser Point, 6050. San Nicolas Island: first rocky outcropping west of sand spit, 4541.

*Laminaria setchellii* is abundant in all surf-swept areas throughout the range on the mainland, forming extensive stands at lowest lower low water level (LLLW). On the Channel Islands it is an excellent indicator of localized cold water.

LAMINARIA SINCLAIRII (Harvey ex Hooker f. et Harvey) Farlow, Anderson et Eaton (1878, no. 118). *Lessonia sinclairii* Harvey ex Hooker f. et Harvey in Hooker (1846, p. 460). *Hafgygia sinclairii* (Harvey ex Hooker f. et Harvey) Areschoug (1883, p. 6). *Laminaria andersonii* Eaton ex Farlow (1876, p. 715, *nomen nudum*). *Laminaria andersonii* Eaton ex Hervey (1881, p. 98). The original description of *Laminaria sinclairii* (as *Lessonia sinclairii*) is meager, but sufficient to validate the name. Failure to accept this description as valid publication would cause *L. andersonii*

*sonii* Eaton ex Hervey to be the correct name for this species, thereby intensifying the nomenclatural confusion between *L. sinclairii* and *L. setchellii*.

Heretofore the known range of *Laminaria sinclairii* has been from Vancouver Island, British Columbia, to San Luis Obispo County, California. The following collections extend this range into Santa Barbara County, California: Point Sal, 5135; Point Pedernales, 2403; Point Conception, 2423; Government Point, 5451, 5519, 5577; Gaviota, 5275. This species apparently is absent on the Channel Islands.

*DICTYONEUROPSIS RETICULATA* (Saunders) G. M. Smith (1942, p. 651, figs. 9–13). Two new localities can be recorded for this strikingly beautiful kelp, previously known only from sublittoral Monterey Bay. Three juvenile plants were collected by an abalone survey team of the California Department of Fish and Game from the Fort Ross cove area of Sonoma County at a depth of 3 to 12 meters, 20 September 1951. Extensive sublittoral stands were discovered off the Channel Islands by the Sefton Foundation Expeditions. One collection was dredged from 31 meters between Fraser Point and Kinton Point, Santa Cruz Island (5884) and another stand was found at a depth of 24 meters  $1\frac{1}{4}$  miles southwest of Ford Point, Santa Rosa Island (5981), both in March, 1950. At Pacific Grove an occasional plant grows in the littoral zone at lowest lower low water level (3044). The blade of the largest plant dredged off Ford Point measured 19 by 107 cm., and this was clearly an incomplete specimen.

It is surprising how steadfastly Setchell refused to recognize the distinctness of this taxon, considering that he himself pointed out the differences between it and *Dictyoneurum* and even illustrated an unmistakable specimen (1896, p. 46, pl. 1).

*EGREGIA* J. E. Areschoug. Of the nine genera of Laminariales restricted to the west coast of North America, *Egregia* alone exhibits much variation. Heretofore, with collecting largely confined to the mainland of California north of Carmel and south of Santa Barbara, there have appeared to be two well-defined species: *E. menziesii* (Turner) Areschoug (1876), extending from Vancouver Island, British Columbia, to Point Conception in Santa Barbara County, California; and *E. laevigata* Setchell (1896), ranging from Point Conception to Baja California, Mexico, with isolated occurrences in Carmel, Monterey County, and Port Harford (Port San Luis), San Luis Obispo County. A study of a long series of specimens from the Channel Islands and the mainland between Carmel and Santa Barbara reveals a more complex picture: in these areas the two species overlap and intergrade, suggesting hybridization.

Typical *Egregia menziesii* has a tough rachis closely beset with simple, entire or dentate, spatulate blades. Short blunt tubercles cover all or most of the rachis (the lowermost portion may be smooth) and frequently also cover the bladders and blades. Typical *E. laevigata* has a smooth brittle rachis, somewhat broader than that of *E. menziesii*, bearing relatively

large, elliptical to ligulate, simple and entire or frequently highly dissected blades. The foliar extension of the bladder, which in *E. menziesii* is stubby, is well developed and ultimately dissected. In the form with the blades dissected into filiform segments, this kelp is known as the "Feather Boa."

Despite the conspicuous differences between typical representatives of the two taxa, when a careful study is made of all available material as to the presence or absence of tubercles and the size, shape, degree of dissection and distribution of blades, the two species are seen to be far less sharply delimited than was previously believed.

Typical *Egregia menziesii* constitutes a remarkably uniform series of populations from Vancouver Island, British Columbia, to Government Point (just south of Point Conception), Santa Barbara County, California. At both ends of the range, however, deviation occurs. On Vancouver Island there is a population with highly dissected blades (Tofino, Clayoquot Sound, *Setchell & Parks*, 23 June 1930; Point No Point, 16 miles west of Sooke, 7053, 17 June 1955). In the vicinity of Point Conception (from Point Pedernales to Government Point) there are plants (2447), putatively hybrid, that show certain characteristics of *E. laevigata* of that area, namely, a smooth rachis (except at the tips of branches) and a wider spacing of blades. No plants referable to *E. menziesii* occur on the mainland south of Government Point, but in the northern Channel Islands plants of *Egregia* consistently exhibit characteristics of the two species combined with intermediate features apparently at random. In the majority of specimens the rachis is tough (not brittle as in *E. laevigata*) and covered in part with tubercles that are longer and more slender than those of typical *E. menziesii*. The blades are variable in size and shape, but in older fronds they become highly dissected, as in *E. laevigata*. Although this series of populations seems to be of hybrid origin and is morphologically heterogeneous, its geographical distinctness supports its recognition as a subspecies. Assignment to one or the other species, however, seems to me to necessitate an arbitrary decision. Thus I arbitrarily refer the Channel Islands subspecies to *E. menziesii*.

*EGREGIA MENZIESII* (Turner) Areschoug subsp. **insularis** subsp. nov. Axis lentus haud fragilis plerumque partim attamen tuberculis gracilibus obtectus paginae frondium maturiorum profunde dissectae.

Rachis tough, not brittle, usually covered at least in part with slender tubercles; blades of older fronds highly dissected.

Type. North shore, West Anacapa Island, Ventura County, Channel Islands, California, 14 March 1950, 6130 (UC 981571).

Additional records. CALIFORNIA. Channel Islands: San Miguel Island: Cuyler Harbor, 3744. Santa Rosa Island: Sandy Point, 4124; mouth of Garañon Cañon, 4104; Bechers Bay, 3235; East Point, 3972. Santa Cruz Island: Fraser Point, *Hubbs* 47-81; Willows Anchorage, 3809, 6047; Smugglers Cove, 6207; Prisoners Harbor, 4140, 5823; Frys Harbor, 3352; Twin Harbors, 3331. Anacapa Islands: *F. H. Elmore*. Santa Barbara Island: landing, 4415; southeast reef, 4354. San Nicolas Island: first rocky outcropping west of sand spit, 4441.

*EGREGIA LAEVIGATA* Setchell subsp. **borealis** (Setchell) stat. nov. *Egregia laevigata* forma *borealis* Setchell (Phyc. Bor. Amer. no. XL, 1901).

Typical *Egregia laevigata* occurs from Goleta, California, to Punta San Eugenio, Baja California, Mexico. Plants clearly referable to *E. laevigata*, yet differing slightly but consistently, are to be found in California from Gaviota, Santa Barbara County, northward to Santa Cruz, Santa Cruz County. The rachis is brittle and usually smooth, although at times the terminal blade, or the young rachis, or both, may bear short blunt tubercles. The blades are similar to those of *E. laevigata*, elliptical to ligulate, but are usually more widely spaced and never dissected. This series of populations as represented at Carmel was described by Setchell as *E. laevigata* f. *borealis*. However, its morphological uniformity and geographical distinctness would seem to warrant its recognition as a subspecies.

In an herbarium annotation, Setchell designated as the type of *Egregia laevigata* a specimen collected by him (1659) at Carmel Bay, Monterey County, California, 17 May 1897 (UC 96743). Inasmuch as this specimen was collected subsequent to the publication of *E. laevigata*, its selection as lectotype is untenable. In the original publication Setchell mentioned plants from Santa Cruz, Port Harford, and San Pedro, all California localities, but only those from San Pedro, Los Angeles County (Setchell 1157, December 1895) have dissected blades, a character emphasized by Setchell. Therefore, it seems reasonable to propose Setchell 1157 as the lectotype collection, and, of several specimens available, UC 96758 as lectotype specimen.

Representative specimens examined. CALIFORNIA. Santa Cruz County: Santa Cruz, C. L. Anderson. Monterey County: Monterey, Setchell 1412 & 3080; Pebble Beach, 1051, 1659, 1799, 3053. San Luis Obispo County: Piedras Blancas, 1376, 5019; Cambria, H. L. Mason; Cayucos, 2313; Port Harford, Setchell 1135; Oilport, Reed 57; Pismo Beach, 5293. Santa Barbara County: Point Arguello, 2517; Government Point, 5454, 5520, 5575; Gaviota, 5229.

A case might well be argued for recognizing in *Egregia* only one species comprised of several subspecies. It seems of greater taxonomic usefulness, however, to continue the recognition of two species.

**Bossiella** nom. nov. *Bossea* Manza (1937a, p. 46).

This genus of Corallinaceae unfortunately bears a name that is a later homonym of *Bossea* in the Geraniaceae, which was proposed by Reichenbach (1841, p. 201) as a substitute name for *Cynosbata* (DC.) Rchb. and commemorates J. F. W. Bosse. The following species seem worthy of recognition.

**Bossiella californica** (Decaisne) comb. nov. *Amphiroa californica* Decaisne (1842, p. 124). As interpreted by Manza (1937b) and Smith (1944), this species is known only from the Monterey Peninsula, California. Yendo (1902b) reported it (as *Cheilosporum californicum*) from Vancouver Island, British Columbia, but the photograph of this collection indicates that most likely Yendo had a sparsely branched specimen of

*B. corymbifera*. The type must be restudied to eliminate the persistent uncertainty as to the identity of this taxon.

**Bossiella cooperi** (Dawson et Silva) comb. nov. *Bossea cooperi* Dawson et Silva in Dawson (1953, p. 158).

**Bossiella corymbifera** (Manza) comb. nov. *Bossea corymbifera* Manza (1937b, p. 562). Heretofore this species has been reported only from the Monterey Peninsula, California (Manza; Smith), and Coos County, Oregon (Doty). The following records amplify the known range.

CANADA. BRITISH COLUMBIA. Vancouver Island: Point No Point, 16 miles west of Sooke, 7047; Victoria, 1875, *R. Middleton*. UNITED STATES. WASHINGTON. Whidbey Island, *Gardner* 918. CALIFORNIA. Mendocino County: Mendocino, *Brown* 754a. Sonoma County: 3 miles north of Fort Ross, *L. Miles*; Horseshoe Cove, near Bodega Bay, *L. Miles*. Marin County: Tomales Head, *W. Hartman*.

**Bossiella dichotoma** (Manza) comb. nov. *Bossea dichotoma* Manza (1937b, p. 562). This species, previously reported only as far north as Moss Beach, San Mateo County, California, has been found at Shelter Cove, Humboldt County (7000).

**Bossiella gardneri** (Manza) comb. nov. *Bossea gardneri* Manza (1937b, p. 563).

**Bossiella insularis** (Dawson et Silva) comb. nov. *Bossea insularis* Dawson et Silva in Dawson (1953, p. 159).

**Bossiella interrupta** (Manza) comb. nov. *Bossea interrupta* Manza (1937b, p. 563).

**Bossiella ligulata** (Dawson) comb. nov. *Bossea ligulata* Dawson (1953, p. 156).

**Bossiella orbigniana** (Decaisne) comb. nov. *Amphiroa orbigniana* Decaisne (1842, p. 124).

**Bossiella pachyclada** (Taylor) comb. nov. *Bossea pachyclada* Taylor (1945, p. 194).

**Bossiella plumosa** (Manza) comb. nov. *Bossea plumosa* Manza (1937a, p. 46). Heretofore this species has been reported only from San Mateo County (Manza) and the Monterey Peninsula (Smith) in California and from southern Oregon (Doty). The following records amplify the known range.

CANADA. BRITISH COLUMBIA. Vancouver Island: Point No Point, 16 miles west of Sooke, 7048. UNITED STATES. WASHINGTON. Jefferson County: Ruby Beach, 7104. OREGON. Lincoln County: Yachats, 7135. CALIFORNIA. Del Norte County: Crescent City, 6902. Humboldt County: Trinidad, 6827. Mendocino County: mouth of Jughandle Creek, 6720. Sonoma County: Shell Beach, 4 miles south of Jenner, 6671; 2 miles north of Bodega Bay, 3496. Marin County: Bolinas, *Gardner* 1026. San Francisco County: Lands End, *Setchell* 5747. Santa Cruz County: Santa Cruz, 3551. Monterey County: mouth of Malpaso Creek, 3632; Kasler Point, 820, 849; Partington Point, 2288; Lucia, 2817. San Luis Obispo County: Cayucos, 2312. Santa Barbara County: Point Pedernales, 2419; Government Point, 5541.

**Bossiella sagittata** (Dawson et Silva) comb. nov. *Bossea sagittata* Dawson et Silva in Dawson (1953, p. 157).

**PACHYARTHRON CRETACEUM** (Postels et Ruprecht) Manza (1937a, p. 45). This North Pacific species extends southward to Vancouver Island, judging from Yendo's photograph (1902b, pl. 51, fig. 1) of a plant collected at Port Renfrew (as *Amphiroa cretacea* f. *tasmanica*).

**CALLIARTHRON REGENERANS** Manza (1937b, p. 565). The following records outline the known range of this species, which heretofore has been reported only from San Mateo County in California (Manza) and Coos and Curry counties in Oregon (Doty).

CANADA. BRITISH COLUMBIA. Vancouver Island: Point No Point, 16 miles west of Sooke, 7045. UNITED STATES. WASHINGTON. Whidbey Island, *Gardner* 83. CALIFORNIA. Del Norte County: Crescent City, 6904. Humboldt County: Shelter Cove, 7002. Mendocino County: mouth of Jughandle Creek, 6717. Sonoma County: Shell Beach, 4 miles south of Jenner, 6670; 2 miles north of Bodega Bay, 3495. Marin County: Bolinas, *Gardner* 1027. Monterey County: Partington Point, 2278; Lucia, 2837. San Luis Obispo County: Piedras Blancas, 5040; Pismo Beach, 5367. Santa Barbara County: Government Point, 2195, 5467, 5511. San Miguel Island: Cuyler Harbor, 3756. Santa Rosa Island: Sandy Point, 4123; Cañada Lobos, 2763; East Point, 4071. Santa Cruz Island: Fraser Point, 5967; Willows Anchorage, 3823, 6039; Smugglers Cove, 6221. Santa Barbara Island: landing, 4405; southeast reef, 4365. MEXICO. BAJA CALIFORNIA. Islas Todos Santos: south island, 4829.

**CALLIARTHRON SCHMITTII** Manza (1937b, p. 566). This rare species, heretofore known only from the San Diego region, has been found on littoral rocks at Eagle Point, San Juan Island, Washington (*Papenfuss & Scagel*, 7 July 1952). The fronds are prostrate, as inferred correctly by Manza from fragmentary dredged material.

**Serraticardia** (Yendo) stat. nov. *Cheilosporum* sect. *Serraticardia* Yendo (1905, p. 2). *Cheilosporum* subgen. *Serraticardia* Yendo (1902c, p. 193, *nomen nudum*). Type species: **Serraticardia maxima** (Yendo) comb. nov. *Cheilosporum maximum* Yendo (1902a, p. 22, pl. 2, figs. 18, 19; pl. 6, fig. 9).

**Serraticardia macmillanii** (Yendo) comb. nov. *Cheilosporum macmillanii* Yendo (1902b, p. 718, pl. 52, figs. 4, 5; pl. 56, figs. 11–14). *Calliarthron pinnulatum* Manza (1937b, p. 565).

This plant, heretofore known only from the original collection made by Yendo in the summer of 1901 at the Minnesota Seaside Station (Port Renfrew), Vancouver Island, has been discovered growing on surf-swept rocks of the lower littoral at two localities in California, namely, three miles north of Fort Ross, Sonoma County (*L. Miles*, 19 July 1951) and Pescadero Point, Monterey Peninsula (3090, 10 July 1948). The regular distichous opposite branching is suggestive of *Corallina*, but the conceptacles are borne laterally on the faces of intergenicula. On axial intergenicula the conceptacles are usually paired, one toward each lateral margin. Pinnae, being of approximately the same width as conceptacles, usually bear only one. According to Yendo, conceptacles may also occur terminally on pinnae, but my material does not show terminal concept-

acles nor are Yendo's figures convincing. Conceptacles borne subterminally on the face of a pinna might easily be misinterpreted as terminal.

The most closely related species appears to be *Cheilosporum maximum* Yendo, from Japan, and both species were placed by Yendo in his section *Serraticardia* (Yendo, 1905, p. 26). Although Manza apparently was not familiar with *Cheilosporum macmillanii*, he (1937b, p. 567) referred *C. maximum* to *Joculator* Manza (1937a, p. 47), a genus based on the character that conceptacles may be both lateral and terminal in the same plant. (*Cheilosporum* as circumscribed by Manza is characterized as having conceptacles only on the upper margins of intergenicula.) *Joculator* was merged into *Corallina* by Dawson (1953, p. 124) on the consideration that lateral conceptacles sometimes occur in *Corallina officinalis* L. *Joculator pinnatifolius* Manza, the type of its genus, has a predominance of terminal conceptacles, and in this character as well as in general habit it seems more closely related to *Corallina* than to either *Cheilosporum macmillanii* or *C. maximum*. In the two latter species lateral conceptacles are the rule rather than the exception, and in habit they seem intermediate between a *Corallina* with compressed intergenicula (e.g., *C. chilensis* Decaisne) and a pinnate *Bossiella* (e.g., *B. plumosa*). In fact, it appears that we are dealing with a group of species which tend to bridge the gap between *Corallina* and *Bossiella*, two genera previously thought to be widely separated. No anatomical differences between these two genera have been demonstrated.

The occurrence of species intermediate between two genera need not affect the taxonomic usefulness and validity of recognizing both genera. In the present case *Cheilosporum macmillanii* and *C. maximum* seem sufficiently similar to one another and sufficiently different from both *Corallina* and *Bossiella* to warrant the recognition of a third genus.

The intergenicula of *Serraticardia* differ from those of *Bossiella* in not being expanded to the point of differentiating wings from the midrib. On the other hand, they are expanded more than those of *Corallina*, resulting in a more closely knit pattern of branching.

The type of *Calliarthron pinnulatum* Manza is a robust but poorly branched specimen of *Serraticardia macmillanii* from Moss Beach, San Mateo County, California (Manza, 2 January 1935). It is surprising that Manza referred this specimen to *Calliarthron*, a genus characterized by a unique anatomy of interwoven filaments.

*PLOCAMIUM OREGONUM* Doty (1947, p. 177, pl. 14, fig. B). According to entries in his notebook, N. L. Gardner had prepared a manuscript for this species and had designated as the type a collection from Trinidad, Humboldt County, California (June 1934, Gardner 7837, UC 536732). The following records supplement those cited by Doty (from Curry, Coos, and Lincoln counties in Oregon and Marin and Humboldt counties in California).

CANADA. BRITISH COLUMBIA. Vancouver Island: Point No Point, 16 miles west of Sooke, 7036. UNITED STATES. CALIFORNIA. Mendocino County: mouth of

Jughandle Creek, 6706. Sonoma County: Shell Beach, 4 miles south of Jenner, 6659; 2 miles north of Bodega Bay, 3510.

Department of Botany,  
University of Illinois,  
Urbana, Illinois

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## A NEW YUCCA FROM SONORA, MEXICO

HOWARD SCOTT GENTRY

*Yucca grandiflora* sp. nov. Arbor 3-4 m. alta; folia 70-100 cm. longa, 4-5 cm. medio lata, viridia, laevia, margine brunneo sparse-filifero, spina terminali valida basi sulcata, 2-2.5 cm. longa; inflorescentia paniculata, ramis lateralibus dense pubescentibus; perianthium subglobosum, segmentis subaequalibus, 7-9 cm. longis, ovatis, mucronatis, glabris; filamenta pubescentia, basi segmentorum adnata; ovarium elongatum, 4.5-6 cm. longum; stylus breviter 3-lobatus; fructum non vidi.

Arborescent, 3-4 m. tall, branching from the base and toward the crown, with deep leaf crowns; leaves 70-100 cm. long, 4-5 cm. wide at mid-blade, slightly narrowed above base, dark green, smooth, ascending to descending, persisting dry and deflected in age on the trunk, the margin narrow, brown, filiferate with long, fine, brittle threads, the terminal spine stout, brown, broadly grooved; inflorescence an irregular open panicle 70-100 cm. long; peduncle 10-30 cm. long, glabrate below; bracts and bractlets scarious, dull white, friable; lateral branches densely white-tomentose, flexuous, horizontal; flowers short-pedicellate to subsessile, glabrous, creamy white, divergent on horizontal, openly-spaced lateral branches (fig. 2); perianth 7-9 cm. long, the segments spreading, ovate, thin, bluntly mucronate, connate at base, the outer slightly smaller and thicker than the inner; filaments hyaline-pubescent throughout, the anthers oblong; pistil slender, 4.5-6 cm. long, deeply sutured, shortly beaked below the lobate stigma; fruits not seen.

Type. Above Tierra Negra, Cedros Range, east of Río Cedros, Sonora, Mexico, February 14, 1952, *Gentry 11601* (U. S. Nat. Herb. 2089433 and 2089434).

This plant differs from all other known species of *Yucca* in the large subsessile flowers borne on tomentose lateral branches in an open ragged-appearing panicle. Although the fruits are not available for study, the obvious relationship is with the group having fleshy fruits, the *Sarcocarpa*.



FIG. 1. Mature clump of *Yucca grandiflora* showing both basal and crownal branching. Above Tierra Negra on the Cedros Range in southern Sonora.

In the rather flexible, long, wide leaves and the pubescent lateral branches of the inflorescence, it resembles *Yucca schottii*. The large flowers and elongate pistils or ovaries, however, relate it more closely to *Y. arizonica*, from which it differs by the 1) pubescent lateral branches of the inflorescence as compared to glabrous branches, 2) subsessile flowers as compared to long-pedicellate flowers, 3) thin, finely veined, ovate perianth segments as compared to thicker, coarsely veined, lanceolate perianth segments, and 4) erect or divergent flowers as compared to nodding flowers.

In the type locality, where it formed a widely scattered colony, *Y. grandiflora* was found associated with species of *Quercus* and *Acacia pennatula* in an extensive tract of Oak Woodland having volcanically derived calcareous soils with a grass cover. Elevations here ranged from about 2500 to 3500 feet. A similar-appearing *Yucca* observed to the southeast of this locality, both along the Arroyo Guajaráy and the Río Mayo in adjacent Chihuahua, may prove eventually to be this species. It is known locally by its Warihio Indian name, "sahuiliqui."

This *Yucca* is one of many collected to determine sapogenin content. The leaves proved to contain 1.4 per cent sarsapogenin, as reported by

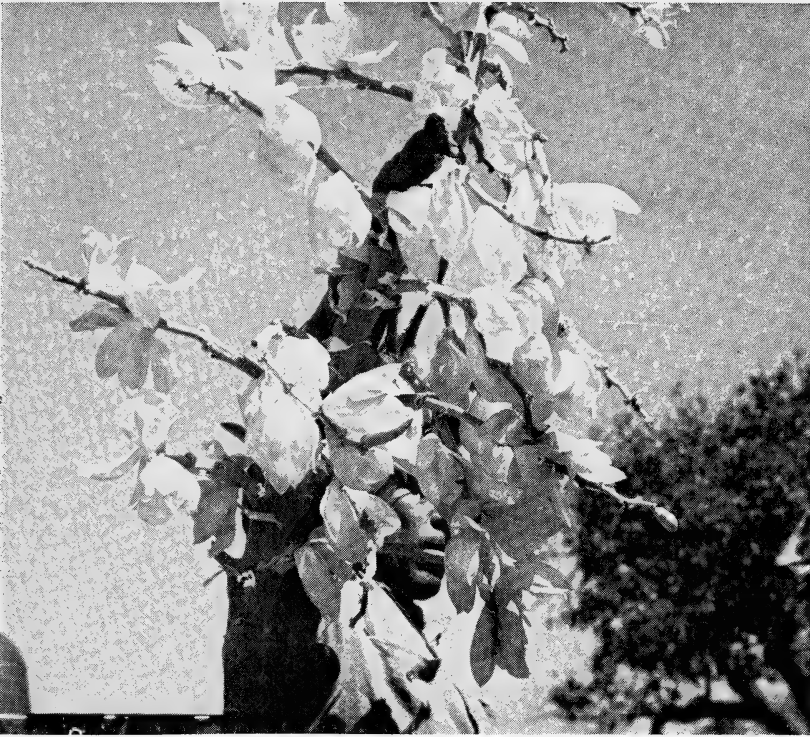


FIG. 2. Type material of *Yucca grandiflora* before pressing. Note the divergent subsessile flowers and the horizontal, openly spaced, lateral branches.

the Eastern Regional Research Laboratory at Philadelphia.<sup>1</sup> Sarsasapogenin is one of the steroidal compounds regarded as precursor to cortisone and related drugs. The fairly high percentage value of sarsasapogenin, together with the fiber in the numerous leaves, indicates an economic potential for *Yucca grandiflora*.

Plant Introduction Section, Horticultural Crops Research Branch,  
Agricultural Research Service, United States Department of Agriculture,  
Plant Industry Station, Beltsville, Maryland

<sup>1</sup> Wall et al. 1955. Steroidal Sapogenins XXVI. Supplementary table of data for steroidal sapogenins XXV. U. S. Dept. Agr., Agr. Res. Serv. Circ. ARS-73-4.

## A REVISION OF THE LUPINUS ARBUSTUS COMPLEX OF THE LAXIFLORI

DAVID B. DUNN

During and prior to the preparation of the manuscript of *Lupinus* for the Flora of Nevada (Dunn, 1956a), the type specimens of over 500 North American lupines, exclusive of species from Mexico, were examined. For each of these types, notes were taken, photographs were made, and floral parts were dissected and mounted in plastic, as described by Dunn (1954). One of the most important groups of type specimens examined was the Lindley collection of Douglas type specimens, Cambridge University (Dunn, 1956b). As a result of the extensive survey of these type specimens, together with careful study of the collection data recorded by Douglas in his journal (1914), it was deemed necessary to make several nomenclatural changes. Some of these were published earlier by me (Dunn, 1955) so that the names would be available for use in the Flora of Nevada. The opportunity now presents itself for discussion of the problems centering around *L. arbustus* and closely related taxa, and for a full explanation of the recombinations pertinent to this complex.

In studying the Douglas type material from the Lindley Herbarium (Dunn, 1956b), I came to the conclusion that Lindley's original description and illustration of *L. laxiflorus* (Bot. Reg. t. 1140, 1828) did not match the specimen labeled *L. laxiflorus* (Douglas 297, fig. 1). Instead, his description and illustration match the specimen labeled *L. tenellus* (Douglas 277, fig. 2). It is only possible to conjecture upon how this error came about. Whether the mixing of the two names occurred as an error by Douglas in collecting ripe seed at a later date than his herbarium sample or as an error when the seeds were planted, it is now impossible to say. In my opinion, however, the description and illustration are critical and must go with the specimen they fit rather than with the specimen which bears the cogent name, particularly for early material collected prior to the adoption of the type concept. (See Appendix 1, paragraph 4a, and Articles 19, 21; International Code, 1952). This interpretation, however, has resulted in the necessity for retypifying *L. laxiflorus*, and for bringing this name (*L. laxiflorus* Dougl. ex Lindl., not Agardh) into synonymy under *L. argenteus* Pursh. subsp. *argenteus* var. *tenellus* (Dougl. ex G. Don) Dunn, since the taxon involved is considered as below specific rank. The reason for the use of the varietal name *tenellus* is simply priority within a given rank (Articles 16, 66, 67, and 70; International Code, 1952). Fortunately *L. argenteus* was published by Pursh in 1814 so the name *L. argenteus* was not upset by recognizing that *L. laxiflorus* was a part of that species. Torrey and Gray were the first to apply a name below the rank of species to the taxon *tenellus* (see number 1 in taxonomic treatment). The " $\gamma$ " used by Torrey and Gray as a prefix to the trinomial



FIG. 1 (left). Photograph of the specimen in the Lindley Herbarium bearing the label *L. laxiflorus*: I have designated this specimen as the type of *L. arbustus* subsp. *neolaxiflorus* Dunn. It does not match Lindley's illustration or description in several important characters (see text).

FIG. 2 (right). Photograph of the specimen in the Lindley Herbarium bearing the label *L. tenellus*. This specimen matches Lindley's description and illustration of *L. laxiflorus* quite closely, with minor deviations (see text). This taxon is treated as *L. argenteus* subsp. *argenteus* var. *tenellus* (Doug. in G. Don) Dunn.

name *tenellus* has generally been conceded to mean a variety since it was not the practice of the time to designate subspecies.

This retypification of *L. laxiflorus* necessitates the redesignation of the taxon classically known as *L. laxiflorus* to subsp. *neolaxiflorus* (Dunn, 1955) and placing it under *L. arbustus* Dougl. ex Lindl. (Bot. Reg. t. 1230, 1829) which is the next specific epithet in line, thus retaining as much continuity of the name as possible. The name *laxiflorus*, then, is no longer spread over five other subspecific taxa, but is restricted to subsp. *neolaxiflorus* specifically, the taxon to which Agardh and botanists since then have been applying the name *laxiflorus* in the strict sense and not in the broad sense employed in current manuals.

The characters of most fundamental importance in interpreting the specimen labeled *L. tenellus* to be the taxon described by Lindley as *L. laxiflorus* are: 1) the short petioles throughout, about as long as the leaf-

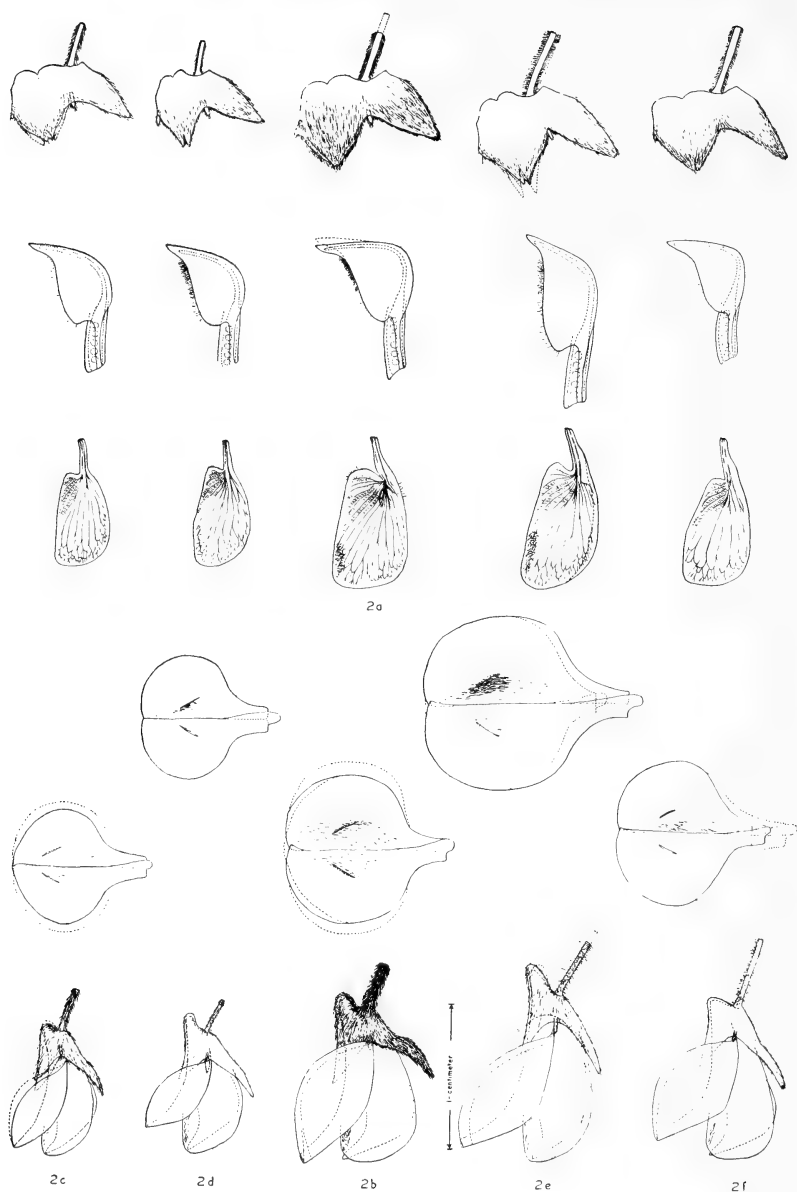


FIG. 3. Chart of the floral parts of the taxa within *Lupinus arbustus*, solid lines drawn to the typical shape and uniform scale of the mean measurements of 25 individuals (numbers 2b, etc., refer to taxa in text and on Map 1). Dotted lines represent parts beneath the surface, folds under the outer surface or, as in the banner and wings, the range of shape. The horizontal rows from bottom to top represent 1) left side view of entire flower; 2) flattened dorsal view of the banner, the two halves showing the range in the amount of pubescence; 3) left wing; 4) right side view of keel;

lets (fig. 2) and illustrated by the artist in Edwards' Botanical Register (t. 1140, 1828); 2) the leaves appearing fasciculate due to the short petioles and to the occurrence of several leaves on the dwarf axillary branches present at most of the nodes at anthesis of the primary racemes; 3) leaflets linear to linear-elliptic-oblongate as illustrated; 4) the slender purplish stems referred to by Lindley; the specimen labeled *tenellus* is distinctly purplish and slender by contrast with the specimen labeled *laxiflorus*; 5) the obcordate shape of the banner described and illustrated; and 6) the floral parts (plastic-coated dissections) match the illustration, t. 1140.

Lindley's statements referring to an absence of bracteoles (in his description of *L. laxiflorus*) and a beardless keel are both erroneous since both of the specimens labeled *L. tenellus* and *L. laxiflorus* have bracteoles and ciliate keels, although the former has the least ciliation. Both also have a spur about 0.5 mm. long at the base of the upper lip of the calyx.

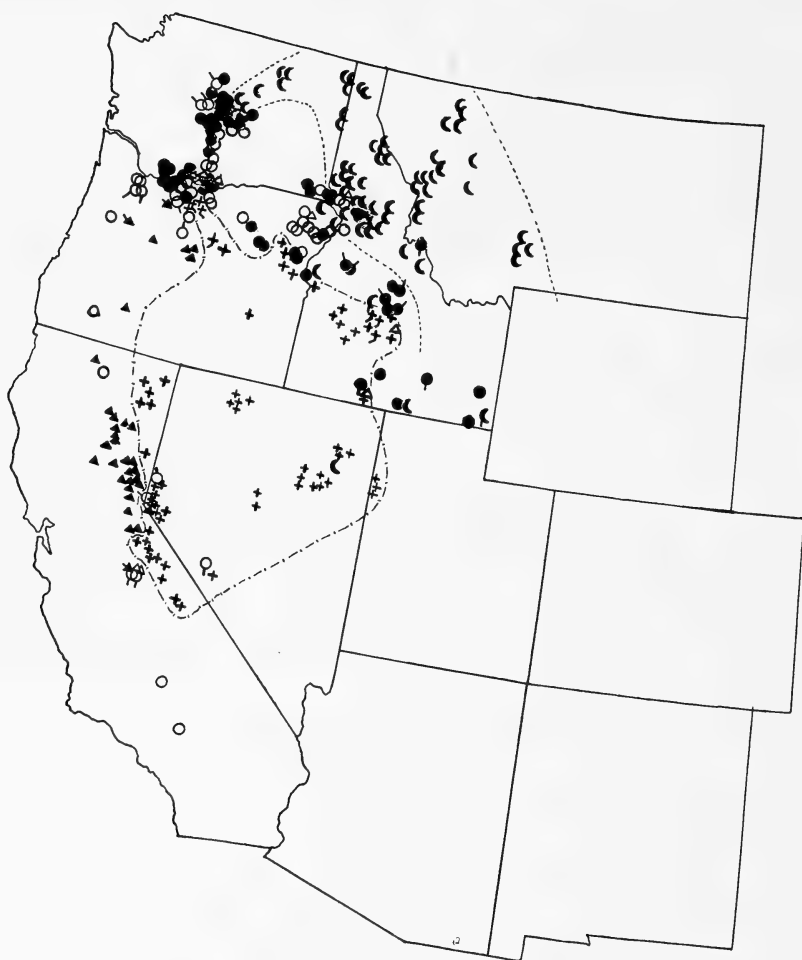
The shape and conformation of the floral parts (fig. 3c, solid lines) were drawn from Douglas 297 (fig. 1), which is considered typical for *L. arbustus* subsp. *neolaxiflorus*. The extent to which the flowers differ from the illustration in Edwards' Botanical Register (t. 1140) should be apparent.

It should be noted that more of the characters which indicate that the specimen labeled *L. tenellus* is the taxon described as *L. laxiflorus* are to be found in the illustration than are found in the description. I dare say this situation is not uncommon among taxa described in either Edwards' Botanical Register or in the Curtis' Botanical Magazine. That the purpose of an illustration is to clarify characters difficult to describe in words is recognized by the Recommendation 54F of Article 54, International Code (1952), where illustrations are recommended. I would contend that where such are provided with the original description that the illustrations are an integral part of the description. The extent to which illustrations are recognized by the Code is noted in Article 21 in which it is stated that an illustration or a description may become the type for a species without a type specimen. It should further be pointed out that the specimens in the Lindley Herbarium considered as types are more technically lectotypes. Thus, Article 19 is involved regardless of who wrote the name *L. laxiflorus* on the specimen (fig. 1). Note again the wording in the International Code (Appendix 1, paragraph 4a, Determination of types); wherein "recognizable figures" are specifically acknowledged as being a means of determining what material has been described.

My interpretation, previously published in outline (Dunn 1955, 1956b), has been questioned by Phillips (1955, p. 196), whose paper came out

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5) inside view of the unfolded calyx cup, slit from the left sinus to the pedicel. Since the floral parts for 2a and 2b are very similar in shape, only the wing is illustrated for 2a (within the 2b series); the wing of 2b is glabrous both laterally and marginally near the claw (not illustrated). Subspecific entities are indicated by the key figures: 2a-2f.



2a. *Lupinus arbustus* subsp. *arbustus* var. *arbustus* ▲

2b. *Lupinus arbustus* subsp. *arbustus* var. *montanus* ○

2c. *Lupinus arbustus* subsp. *neolaxiflorus* ●

2d. *Lupinus arbustus* subsp. *silvicola* ▲

2e. *Lupinus arbustus* subsp. *calcaratus* + — — — —

2f. *Lupinus arbustus* subsp. *pseudoparviflorus* ☾ - - - - -

Intermediates or hybrids ○ ● † ▲

FIG. 4. Distribution of the taxa within *Lupinus arbustus*.



after I had submitted this present manuscript for publication in June, 1955. Phillips admits that Lindley's description of *L. laxiflorus* does not fit the specimen labeled *L. laxiflorus*, but he believes the latter to be labeled in Lindley's handwriting, whereas I am convinced it is in Agardh's. Phillips borrowed only the types designated as *L. tenellus* and *L. laxiflorus*. Phillips fails, however, to recognize the significance of the coincidence of morphological characters in Lindley's description and illustration of *L. laxiflorus* with the characters shown in the specimen labeled *L. tenellus*, nor does he recognize the significance of the characters which differentiate the specimen labeled *L. tenellus* from the specimen labeled *L. laxiflorus*.

Phillips, in other words, relies on what has been presumed to be the type specimen irrespective of the facts that the authorship of the handwriting thereon is uncertain and that neither the type description nor the illustration fits this presumed type specimen. It should be emphasized that the type concept was not accepted in Europe until the 1930's, after which time type labels were placed on specimens by current workers; sometimes sheets with type material were cut apart and the parts mounted on separate sheets; and, in one case of which I know, the type label was transferred to the wrong half of the sheet. There has been too much chance for error in the processing and reprocessing of the early specimens. With this early material it is not the specimen considered as the type itself, but the description and illustration which are critical, as noted repeatedly in the International Code (1952, Articles 19, 21, and Appendix 1). In the case of the lupines under consideration, I have made a considerable effort, as already stated, to clarify these matters and to coordinate the type localities as given in Douglas' Journal (Dunn, 1956b) with the type specimens in the Lindley Herbarium and with their published descriptions.

The taxonomic problems involved with the treatment of lupines have been multiplied considerably since settlement of western North America. Extensive cattle grazing undoubtedly created numerous openings, and in more recent years the great increase of roads has greatly multiplied the disturbed areas. Lupines are early invaders in areas very low in soil nitrogen such as the exposed subsoils of road cuts or areas vacated by receding glaciers (Lawrence, verbal communication, 1950). Road cuts are commonly inhabited by lupines, a site inadequate for most plants lacking a means of nitrogen fixation. Several species, normally perennial but capable of maturing seed in one season, are now commonly found scattered through grainfields. Such extensions of suitable habitat have undoubtedly resulted in many range extensions during the past hundred years, thus bringing taxa into contact which may have appeared quite distinct in Douglas' time, but which had not been segregated sufficiently long to develop adequate barriers to hybridization. The study of the taxa of *Lupinus* encompassed in the Flora of Nevada has revealed that there are occasional morphological intermediates between many of the closely related taxa.

Many of these intermediates have been collected since settlers and mechanization have come to the country. While it is readily admitted that collecting conditions became simpler with the advent of roads, accounting for increased knowledge of the genus, another explanation must also be considered as possible, if not probable, for the occurrence of morphological intermediates. This is Edgar Anderson's theory of introgressive hybridization (1949), which appears to fit the situation well. His explanation of the survival of hybrid swarms gives a plausible reason for the existence of these intermediates, although it is questionable if they do more than survive long enough to permit some gene flow between what are otherwise well-established taxa with genomes that have been selected by the environment over a long period of time. The question arises as to how to deal taxonomically with these intermediates. If all the taxa which have intermediates between them were placed in one species, the genus *Lupinus* would be reduced to a handful of species, but the keys to separate the subspecific taxa would indeed be complex. I believe it is far better to treat many of the taxa as ecospecies in the sense advanced by Anderson.

At this point I wish to express my appreciation to the officials of the herbaria cited in the text below for the loan of the material and especially to Dr. P. A. Munz for the use of the facilities at the Rancho Santa Ana Botanic Garden where most of the work on this paper was done.

#### KEY TO THE TAXA

Petioles all short, 2-4 cm. long, the lower ones commonly not much longer than the leaflets, occasionally up to 8 cm. long; leaves cauline; banner obcordate to orbicular, sparsely pubescent in the dorsal grooves; the wings glabrous; calyx spur generally wanting, short but present in *L. argenteus* subsp. *argenteus* var. *tenellus*. (*Lupinus argenteus* and allies; not treated here except for the nomenclature of the var. *tenellus*).....1. *L. argenteus* subsp. *argenteus* var. *tenellus*

Petioles gradated, the lower ones 8-15 cm. long, to 2-4 cm. long on the uppermost leaf; commonly mostly basal leaves but members of some taxa with the leaves all cauline, then with the longest lower petioles over 10 cm. long; banner obovate to orbicular; calyx spur generally well-developed, except in *L. sulphureus* and allies.

Banner glabrous (a few individuals with some pubescence on the back); wings glabrous; the base of the calyx enlarged, gibbous above, not spurred.

.....*L. sulphureus* and allies, not treated here.

Banner generally abundantly pubescent over the central area of the back, sometimes only sparsely pubescent in the grooves or sometimes glabrous; wings generally with lateral pubescence near the tip but sometimes glabrous in members of two taxa; calyx spur generally well-developed.

Leaflets glabrous above, or glabrate, oblanceolate, 6-10 mm. wide, banner and wings pubescent or often glabrous; in damp habitats; northeastern Washington and the Rocky Mountains.....2f. *L. arbustus* subsp. *pseudoparviflorus*

Leaflets pubescent above, sparsely so in some, generally linear-elliptic, to oblanceolate, banner and wings pubescent, or often glabrous in subsp. *neolaxiflorus*; California, Nevada, Oregon, Washington and the southern half of Idaho.

Flowers 6.5-9.5 mm. long, excluding the spur.

Plants 2-4 dm. tall, stems clumped, generally with several long-petioled (8-12 cm.) basal leaves; wings and banner glabrous or pubescent; Wenatchee Mountains, Washington, south-eastward into the Snake River drainage of southern Idaho (specimens from the southeastern part of the range exhibit a reduction in the number of basal leaves and an increase in pubescence and height of plant).

.....2c. *L. arbustus* subsp. *neolaxiflorus*

Plants 4-5 dm. tall, stems few, with few or no basal leaves, the leaves oblanceolate or narrowly so, sparsely pubescent above; wings pubescent at the tip; spur somewhat slender; banner orbicular, pubescent in the dorsal grooves; northern Sierra Nevada, California, and Cascade Mountains, Oregon.....2d. *L. arbustus* subsp. *silvicola*

Flowers 9.0-14 mm. long, excluding the spur; banner and wings pubescent, the banner rarely glabrous.

Flowers 11-14 mm. long, generally white or light yellow to lavender (see also var. *montanus*), intermediates bright purplish blue; calyx spur slender, 1-3 mm. long; upper lip generally 6-7 mm. long; wings and flower slender, viewed laterally; Great Basin.

.....2e. *L. arbustus* subsp. *calcaratus*

Flowers 9-12 mm. long; purplish blue to pinkish lavender, drying blue; calyx spur blunt and broader, 1-1.5 mm. long; upper lip 5 mm. long; wings 4-5 mm. wide, the flowers appearing wider; mountains of northeastern Oregon and southward into the southern Sierra Nevada, California.

Wings with pubescence laterally near the apex only.

.....2b. *L. arbustus* subsp. *arbustus* var. *montanus*

Wings with pubescence as above but also with cilia above or below the claws or with lateral villi on the veins near the claws, or with hairs at all three locations.....2a. *L. arbustus* subsp. *arbustus* var. *arbustus*

1. *LUPINUS ARGENTAEUS* Pursh subsp. *ARGENTAEUS* var. *TENELLUS* (Dougl. in G. Don) D. Dunn, Leaf. West. Bot. 7:254. 1955. (G. Don cites Dougl. mss. but the description is not a copy of anything in Douglas' Journal; some other mss?). Type. *Douglas* 277, 31 May 1825 (CGE), p. 125 in Douglas' Journal, collected from the vicinity of the Grand Rapids of the Columbia River, Washington or Oregon ( $\pm 40$  miles "?", Douglas' hiking range). *Lupinus laxiflorus* Dougl. ex Lindl. not Agardh, Bot. Reg. t. 1140. 1828. *Lupinus tenellus* Dougl. in G. Don, Gen. Hist. Dichl. Pl. 2:367. 1832. *Lupinus laxiflorus* var. ("γ") *tenellus* (Dougl. in G. Don) Torr. & Gray, Fl. N. Am. 1:377. 1840 (*L. foliosus* var. ("β") *stenophyllus* Nutt. mss. *ibid.* in syn.). *Lupinus stenophyllus* Nutt. ex Rydb. Bull. Torrey Club 34:42. 1907. *Lupinus argenteus* var. *stenophyllus* (Nutt. ex Rydb.) Davis, Flora Idaho, 492. 1952. *Lupinus lanatocarinatus* C. P. Smith, Sp. Lup. 317. 1942 (an intermediate with *L. caudatus* Kell.). Type. East of Fort Hall, Bingham County, Idaho, *Davis* 137-35 (IDS). *Lupinus fremontensis* C. P. Smith, Sp. Lup. 320. 1942. Type. Sand dunes 6 miles northwest of St. Anthony, Fremont County, Idaho, *Davis* 326 (DS, isotype at IDS). *Lupinus edward-palmeri* C. P. Smith, Sp. Lup. 572. 1946. Type. Big Butte Station, Idaho, *Palmer* 558 (US). *Lupinus carciiformes* C. P. Smith, Sp. Lup. 574. 1946. Type. Four miles south of Macks Inn, Fremont County, Idaho, *Christ & Ward* 14899 (DS, isotype at NY).

*Lupinus hullianus* C. P. Smith, Sp. Lup. 573. 1946. Type. From a burn, Clark County, Idaho, *Hull* 235 (USFS 91141, co-type DS-Sm.).<sup>1</sup> *Lupinus montis-cookii* C. P. Smith, Sp. Lup. 726. 1952. Type. Cook Mountain, Clearwater Forest, Idaho, *Sutton* 70 (USFS 38580).

A detailed description is not presented here, since it is considered that such properly belongs in a monographic treatment of the "argenti" which will be presented at a later date. The name *tenellus* has priority at the rank of variety. The name *stenophyllus* may require recognition at some rank below the level of species when the type specimen is located. It is not possible to separate the two as Rydberg did, since the type of *tenellus* has a distinct but short spur, which Rydberg used to characterize *stenophyllus*. Hence, the treatment of var. *stenophyllus* as a synonym of var. *tenellus* as given in Torrey and Gray's Flora of North America appears correct. The short spur, however, led Torrey and Gray to place the variety *tenellus* in the species *L. laxiflorus sensu* Agardh. The taxon *tenellus* (*L. laxiflorus* of Lindl.) belongs in the species *argenteus*, as pointed out by Davis (Fl. Idaho, 1952), because of the shape of the banner. There is also a light patch of ciliation on the back of the banner under the lip of the calyx, a character which occurs consistently throughout the *L. argenteus* complex (except in *L. rubricaulis*). The pubescence on the back of the banner in the *L. arbustus* group ranges from none to an extensive area on the back.

2a. *Lupinus arbustus* Dougl. ex Lindl. Bot. Reg. t. 1230. 1829 (subsp. *arbustus* var. *arbustus*). Lindley wrote "... local ... gravely soils in North California, ... common near Fort Vancouver ..." This statement is in error. Douglas went to California on December 22, 1830. The notes in Douglas' Journal (1914) matching this taxon place the type region near Falls of the Columbia (Celilo Falls, Klickitat County, Washington or Wasco County, Oregon), *Douglas* 296, 20 June 1825 (CGE). *Lupinus laxiflorus* var. *arbustus* (Dougl. in Lindl.) M. E. Jones, Contrib. West. Botany 14:33. 1912. *Lupinus laxiflorus* var. *laxiflorus sensu* Phillips *pro parte*, Res. St. State Col. Wash. 23:196. 1955.

Plants 3–6 dm. tall; dry stems 3–4 mm. in diameter, finely sericeous to densely subappressed-sericeous; lower petioles 8–13.5 cm. long, present at flowering or the leaflets fallen; leaflets of the largest leaves 8–12, 4–5.5 cm. long, 5–8 mm. wide, linear-oblongate, tending to be conduplicate, arcuate, the tips acute; peduncles 3–5 cm. long; flowers 10–12 mm. long; base of the upper calyx lip developed into a distinct spur 1–1.5 mm. long; banner reflexed above the midpoint, pubescent over the central area of the back and pubescent in the ventral sulcus near the umbos; wings with lateral pubescence near the tip and also with lateral villi on the veins near the claws and ciliation on the edges above and below the claws; keel

<sup>1</sup> DS-Sm.=C. P. Smith Herbarium in the Dudley Herbarium, Stanford University. All other abbreviations of herbaria follow Lanjou & Stafleu, Index Herbariorum 2. 1952.

densely ciliate near the acumen and sparsely so above the claws, also with lateral villi near the claws; ovules 4–5; mature pods not seen.

The variety *arbustus* in its typical form appears to be of rare occurrence. Unfortunately the specific name was applied by Douglas to a plant (*Douglas 296*), which appears to be of hybrid origin or perhaps ancestral to, or at least lying between, *L. caudatus* Kell. and the rest of the complex treated here as *L. arbustus*, of which *L. arbustus* subsp. *neolaxiflorus* Dunn represents an extreme. The floral characters of the type specimen, *Douglas 296*, in the Lindley Herbarium combine traits of *L. caudatus* (which has lateral villi near the claws of the wings and keel and marginal cilia above and below the claws of both the wings and keel, the hairs occasionally absent at two or three of the six locations) with those of the various subspecies treated here under *L. arbustus* (which have a patch of pubescence laterally near the tip of the wings, commonly absent in a percentage of two subspecies). The vegetative affinity and nature of the pubescence of the plant are both very close to var. *montanus* which grades into subsp. *neolaxiflorus* in one direction and subsp. *calcaratus* in the other direction.

The specimens of more recent collection which match the specimen *Douglas 296* are from what appears to be a local endemic population in the mountains of Klickitat County, Washington. This suggests that Douglas collected both 296 and 297 in that area, but it is possible that a similar population may exist or have existed on the south side of the Columbia River in Wasco County, Oregon.

The taxon *L. caudatus* was observed to be sympatric with *L. arbustus* subsp. *calcaratus* (Kell.) Dunn, but there appears to be a barrier to hybridization since no intermediates were observed in herbarium material. Hence *L. caudatus* was retained in its present status, rather than reducing it to a subspecies of *L. arbustus*. *Lupinus caudatus* appears to hybridize with several of the other subspecific taxa within *L. arbustus*, however, and thus may form one end of an overlapping ring of subspecies as discussed by Goldschmidt (1952, p. 90). Since the present evidence suggests that *L. caudatus* may be an ecospecies, it was considered that breeding studies would be necessary before reaching a decision involving any change in status of *L. caudatus*. Judging from the number of morphologically intermediate herbarium specimens seen, *L. caudatus* also appears to hybridize with several other less closely related taxa than those mentioned above.

Some anomalies have resulted from what appears to have been hybridization between *L. caudatus* and *L. arbustus* subsp. *silvicola* and secondly, *L. caudatus* and *L. arbustus* subsp. *neolaxiflorus*, such anomalies resembling *L. arbustus* subsp. *arbustus* var. *arbustus*, but being well beyond the range of the typical material as well as showing vegetative affinities with the suggested parents. Five such specimens are: 1) *Congdon* (MIN), July 25, 1891, Independence Mountains of Cassia County, Idaho; 2) *Christ 14486* (NY), from the same place; 3) *Lyle* (DS), August, 1930, 7 miles south of Lick Ranger Station, North Fork, Wallowa River, Wal-

Iowa County, Oregon; 4) *Congdon* (MIN), near Inspiration Point, Yosemite, Mariposa County, California; 5) *Shoop 94* (UMO), Majic Dam, Hailey, Blaine County, Idaho.

Distribution. WASHINGTON. Klickitat County: vicinity of the Falls of the Columbia, *Douglas 296* (see type citation); hillsides at top of grade from Roosevelt to Bickelton (flowers deep wine-red), *Pickett, McMurray, & Dillon 1441* (WS); western Klickitat County (near Bingen?), *Suksdorf 39* (WS); Columbus, *Suksdorf 1792* (WS).

2b. *LUPINUS ARBUSTUS* subsp. *ARBUSTUS* var. *MONTANUS* (Howell) Dunn, Leaf. West. Bot. 7:254. 1955. *Lupinus laxiflorus* var. *montanus* Howell, Erythraea 3:33. 1895. Type. Mount Hood, Oregon, *T. Howell 1494* (isotype, UC, MO). *Lupinus laxiflorus* var. *cognatus* C. P. Smith in Jepson, Man. Fl. Pl. Calif. 527. 1925. Type. Wallowa Mountains, Oregon, *Cusick 3187* (DS). *Lupinus lutescens* C. P. Smith, Sp. Lup. 235. 1940. Type. Badger Mountain, Douglas County, Washington, *Thompson 14626* (WTU). *Lupinus proteanus* Eastw. Leaf. West. Bot. 4:190. 1945. Type. Emigrant Pass, Nevada, *Eastwood & Howell 231* (CAS). *Lupinus perconfertus* C. P. Smith, Sp. Lup. 738. 1952. Type. Lemhi Nat. Forest, Horse Heaven Pass, Idaho, *Cusick 59* (USFS 56696). *Lupinus laxiflorus* var. *laxiflorus sensu* Phillips *pro parte*, Res. St. State Col. Wash. 23:197. 1955.

Plants 3–6 dm. tall; dry stems 2.5–3.5 mm. in diameter, clustered, from a woody caudex, sericeous; longest lower petioles 9–16 cm. long, present at anthesis; leaflets of largest leaves 9–13, 3–4.5 cm. long, 5–7 mm. wide, linear-elliptic to linear-oblongate, densely or finely sericeous on both sides, tending to be conduplicate, arcuate, on drying; peduncles 3–5 cm. long; flowers 10–12 mm. long; spur at base of calyx 1–1.5 mm. long; banner reflexed above the midpoint, pubescent over the central area of the back and in the ventral sulcus near the umbos; wings with lateral pubescence near the tip but glabrous on the basal half; keel ciliate along the upper margins but otherwise glabrous; ovules 4–5; pods 20–30 mm. long, 6–8 mm. wide, sericeous to villous.

The variety *montanus* is morphologically very close to the variety *arbustus*. The variety *montanus* is the more common of the two, and the vegetative appearance is more nearly that of a robust subsp. *neolaxiflorus*. The var. *montanus* is found on rocky or gravelly montane slopes with yellow pines or at higher elevations. The smallest specimens of var. *montanus* are from Kittitas County, Washington, where the vegetative characters resemble those of subsp. *neolaxiflorus*, but the flower conformation is typical of var. *montanus*. The specimens cited from Douglas and Chelan counties, Washington (*L. lutescens* C. P. Sm.), morphologically belong with var. *montanus* but apparently there has been introgression from *L. sulphureus*. The white color makes this population look very much like subsp. *calcaratus*, which blends into var. *montanus* across the northern part of Oregon.

Distribution. (partial citation, see Map 1). CALIFORNIA. Kern County: Shirley Creek, Greenhorn Mountains, *Griffith 464* (POM). Los Angeles County: Swartout

Valley, San Gabriel Mountains, *Munz* 4607 (POM). Mariposa County: 8 miles west of Glacier Point, *Wiggins* 9224 (POM). Siskiyou County: north of Weed, June 12, 1940, *Lewis* (LA).

IDAHO. Adams County: Smith Mountain, *Davis* 2539 (WS). Nez Perce County: Culdesac, May 20, 1932, *Warren* (WS). County?: Craig Mountains, Sandberg, *MacDougal & Heller* 226 in part (POM).

NEVADA. Douglas County: Spooner, June 23, 1902, *Baker* (POM). Esmeralda County: Emigrant Pass, *Eastwood & Howell* 231 (CAS).

OREGON. Baker County: Cornucopia, slopes of Wallowa Mountains, *Thompson* 13343 (RSA, WS). Powder River Mountains, August, 1896, *Piper* (WS). Benton County: near Corvallis, June 19, 1898, *Kincaid* (WS). Clackamas County: (both the following are probably hybrids with subsp. *silvicola*) opposite Oswego, May 24, 1888, *Millard* (WS); Oswego, May, 1889, *Drake & Dickson* (WS). Gilliam County: 3 miles south of Olex, *Hitchcock* 19218 (RSA & WS). Jefferson County: Cove Palisade, 13 miles southwest of Madras, *Cronquist* 6942 (RSA). Morrow County: between Spray and Hardman, Blue Mountains, *Cronquist* 6618 (RSA). Multnomah County: Willamette River, below Portland, *Sheldon* 510858 (POM, MO, WS). Sherman County: DeMoss, *Hill* 7; 49 (WS). Union County: source of Two Color Creek, Wallowa Mountains, *Cusick* 3187 (MO, WS), 3668 (WS), 3690 (RSA, WS); vicinity of Union, *Cusick* 3714 (WS). Wallowa County: Lookout Mountain, Hell's Canyon, *Constance & Jacobs* 1424 (WS). Wasco County: 5 miles east of Oregon Skyline Trail, Highway 50, *Martin* 4815 (RSA, LA, MO, & WS) (an intermediate with subsp. *silvicola*); 25 miles south of Maupin, *Peck* 26162 (WS); The Dalles, *Suksdorf* 1959, 1961, 1962, 1968, 2185 (WS).

WASHINGTON. Asotin County: south of Puffers Butte, *Cronquist* 5818 (RSA & WS) (probable hybrid). Chelan County: Wenatchee Mountains, *Hitchcock* 17285 (RSA & WS), *Griffiths & Cotton* 127 (WS). Wenatchee, *Whited* 41, 1103 (WS); 25 miles southeast of Wenatchee, *Pickett* 1271 (WS). Douglas County: slopes of Badger Mountain, *Thompson* 14626 (WTU). Kittitas County: Table Mountain, *Thompson* 14887a in part (RSA); Bald Mountain, *Thompson* 14806 (RSA). Klickitat County: Columbus, *Suksdorf* 6498 (MO, WS), 6512 (WS); Rockland, Klickitat Mountains, *Suksdorf*, June 12, 1893 (WS), 2306 (MO). Yakima County: Yakima Indian Reservation, Medicine Valley, *Heidenreich* 94 (WS).

2c. LUPINUS ARBUSTUS subsp. NEOLAXIFLORUS Dunn, Leaf. West. Bot. 7: 254. 1955. Type. Vicinity of the Falls of the Columbia River (Celilo Falls, probably in Klickitat County, Washington, but also possibly on the south side of Columbia River, Wasco County, Oregon, perhaps as much as 20–40 miles inland, Douglas' hiking range), *Douglas* 297, 20 June 1825 (CGE). *Lupinus laxiflorus sensu* Agardh, *pro parte*, Syn. Gen. Lup. 1835 (not *L. laxiflorus* Dougl. ex. Lindl.). *Lupinus laxiflorus sensu* Torrey and Gray, *pro parte*, Fl. North America, 1840, likewise for the other authors covering western North America (1840–1951). *Lupinus inyoensis* var. *demissus* C. P. Smith, Bull. Torrey Club 51:304. 1924. Type. Wallowa Mountains, Baker County, Oregon, *Peck* 5329 (WILL. U.; cotype, DS.). *Lupinus caudatus* var. *submanens* C. P. Smith, Sp. Lup. 106. 1939. Type. Antone Creek, 2 miles east of Anthony Lake, Wallowa County, Oregon, August 10, 1930, *Lyle* (DS). *Lupinus lyleianus* C. P. Smith, Sp. Lup. 107. 1939. Type. Seven miles east of Pearson Ranger Station, Umatilla National Forest, Oregon, July 14, 1930, *Lyle* (DS) (an intermediate with *L. caudatus*). *Lupinus yakimensis* C. P. Smith, Sp. Lup. 238. 1940. Type. Cleman Mountains in alpine sagebrush, 25 miles north-

west of Yakima, Washington, *Thompson 14572* (WTU). *Lupinus wenatchensis* Eastw., Leaf. West. Bot. 3:174. 1942. Type. Alpine slopes of Wenatchee Mountains, *Thompson 14242* (CAS). *Lupinus henrysmithii* C. P. Smith, Sp. Lup. 566. 1946. Type. Minidoka National Forest, Idaho, *H. L. Smith 119* (USFS 42539). *Lupinus amniculi-putorii* C. P. Smith, Sp. Lup. 575. 1946 (an intermediate with *L. caudatus* Kell.). Type. Mink Creek, Bannock County, Idaho, July 30, 1935, *Crane* (DS). *Lupinus mackeyi* C. P. Smith, Sp. Lup. 725, 1952. Type. Clifty Block Mountain Range, Kaniksu National Forest, Idaho, *Mackey 65* (USFS 47532). *Lupinus augusti* C. P. Smith, Sp. Lup. 733. 1952 (an intermediate with *L. caudatus* Kell.). Type. Head of Slater Creek, Boise National Forest, Elmore County, Idaho, *Pearce 23* (USFS 64136). *Lupinus stipaphilus* C. P. Smith, Sp. Lup. 733. 1952. Type. North Star Lake, Boise National Forest, Elmore County, Idaho, *Pearce 165b* (USFS 67739). *Lupinus festucasocius* C. P. Smith, Sp. Lup. 738. 1952 (an intermediate with *L. caudatus* Kell.). Type. Copper Basin Potholes, Lemhi National Forest, Idaho, *Johnson 20* (USFS 56432). *Lupinus stockii* C. P. Smith, Sp. Lup. 743. 1952. Type. Bostetter Ranger Station, Minidoka National Forest, Idaho, *Stock 186* (USFS 33836). *Lupinus standingi* C. P. Smith, Sp. Lup. 749. 1952. Type. Deep Creek, near Malad, Cache National Forest, Idaho, *Standing 18* (USFS 44296). *Lupinus laxiflorus* var. *laxiflorus sensu* Phillips *pro parte*, Res. St. State Col. Wash. 23:197. 1955.

Plants 2–4 dm. tall, the stems clumped from a woody caudex, the upper nodes branching later, finely sericeous throughout, the petioles of the basal leaves 8–13 cm. long, slender, present at anthesis; leaflets 8–10, linear-elliptic to linear-oblongate, the largest 2.5–5 cm. long, 3–7 mm. wide, pubescent on both sides, the tips acute; peduncles 2–8 cm. long; racemes 7–12 cm. long, lax or dense; bracts subpersistent to caducous; verticels 8–20 mm. distant; pedicels 3–4 mm. long; flowers 8–10 mm. long; upper lip of the calyx 3–4.5 mm. long, with a gibbous base or a short spur 0.2–1.4 mm. long at the base, the lip exposed or partially covered by the sides of the banner, with bracteoles 0.2–1 mm. long; banner obovate to suborbicular, sparsely pubescent in the dorsal grooves and under the calyx lip, or glabrous in about one-fourth of those studied; wings pubescent laterally near the tip in about one-third of those seen, more commonly glabrous; keel minutely and sparsely ciliate along the upper edges; ovules 3–5; pods 24–28 mm. long, 6–7 mm. wide, silky-sericeous.

Included in *L. arbustus* subsp. *neolaxiflorus* is the main mass of material considered by authors since Agardh as *L. laxiflorus*. Its center of distribution is in the mountains of central Washington, extending southward into the northern edge of Oregon and eastward in the Snake River drainage of southern Idaho. It is found in meadows and gravelly valleys and in rolling hills with *Artemisia tridentata* and *Tetradymia*, and on up to rocky slopes in the Ponderosa Pine zone. Some specimens appearing to be hybrids with subsp. *pseudoparviflorus* were collected among aspens and lodgepole pines.



The smaller vegetative habit and the smaller flowers, as well as the fact that the flowers commonly have glabrous wing tips, less pubescence on the back of the banner, and sparse ciliation on the upper edges of the keel, all suggest a close relationship with *L. lepidus*. The vegetative stature of two specimens from Kittitas County, Washington (*Thompson* 14806, 14887, cited under var. *montanus*) and the wing pubescence on the wing tips of some of the individuals from the Wenatchee Mountains (*Hitchcock* 17285), both suggest gene flow between *L. arbustus* var. *montanus* and subsp. *neolaxiflorus*.

Distribution (partial citation). IDAHO. Blaine County: Corral Creek, 15 miles up Morgan Creek, *Hitchcock* 14125 (RSA). Smoky Mountains, *Macbride & Payson* 3754 (POM). Cassia County: 22 miles east of Rogerson, Goose Creek Mountains Division, *Christ* 18490 (NY). Custer County: Salmon River Mountains near Bonanza, *Macbride & Payson* 3392 (POM); 28 miles southeast of Patterson, *Christ* 17809 (NY). Franklin County: Franklin Basin, head of Cub River, *Christ* 16366 (NY). Gooding County: Gooding, *Shoop* 117 (UMO) (with some traits of subsp. *pseudoparviflorus*). Idaho County: Heaven's Gate, Seven Devil Mountains, *Q. Jones* 215 (RSA). Jerome County: 14 miles west of Eden, *Christ* 15420 (NY). Power County: Crystal, 19 miles southwest of Pocatello, *Christ* 18559 (NY, an intermediate with *L. caudatus*). Twin Falls County: 12 miles east of Rogerson, *Christ* 18485 (NY). Washington County: 17 miles northwest Mann Creek Store at 4th of July Creek, *Christ* 17943 (NY).

OREGON. Baker County: Eagle Creek, Wallowa Mountains, *Cusick* 2331a (WS); ridge south of Anthony Lake, Elkhorn Range, *Maguire & Holmgren* 26904 (POM & WS); 12 miles northwest of Unity, *Hitchcock* 19464 (RSA). Grant County: Indian Springs Road to Strawberry Peak, Blue Mountains, *Maguire & Holmgren* 26857, 26858 (WS). Hood River County: 5 miles west of Hood River, *Cooke* 17342 (WS); Hood River, *Suksdorf*, June 15, 1883 (WS). Multnomah County: Bonneville, *Suksdorf* 1793, 1797 (WS), *Hill* 70 (WS). Wasco County: Friend, *Hill* 29, 56 (WS); The Dalles, *Suksdorf* 2184 (WS). Union County: Two Color Creek, Wallowa Mountains, *Cusick* 3692 (WS).

WASHINGTON. Asotin County: road to Blue Mountains, 6 miles from Anatone, *Downen* 100 (WS); Anatone, *St. John* 9561 (WS); opposite Zindel, *St. John & Rex Brown* 3225, 3691 (WS). Chelan County: Boulder Peak, *Thompson* 11787 (POM); Tronson Ridge, *Thompson* 9320 (POM, MO); Alpine Ridge near Mt. Stuart, *Thompson* 9513 (RSA). Columbia County: one mile east of Table Rock, Umatilla National Forest, *Kruckeberg* 2524 (RSA). Douglas County: Badger Mountain, northeast of Wenatchee, *Hitchcock* 17387 (WS). Kittitas County: Lion Lookout Station, Table Mountain, *Hitchcock*, *Rethke & van Raadshooven* 3616 (LA, RSA, POM & WS); ridge east of Virden, *Thompson* 11588 (POM, WS, MO); Salom La Sac, *Thompson* 10464 (POM, MO); Iron Mountain, *Thompson* 10039 (RSA); hillsides near Yakima River at Cle Elem, *Benson* 1257 (POM); Beverly Creek, *Thompson* 10039 (POM); Wenatchee Mountains, *Thompson* 14242 (WS). Klickitat County: Falls of the Columbia, *Douglas* 297 (refer to citation of type); Klickitat, *T. Howell*, May, 1870 (WS); Bingen vicinity, *Suksdorf* 10519, 12387, 10491, 10492 (WS); Falcon Valley, *Suksdorf* 347; 2569; 7284; 8280 (WS). Skamania County: Dog Creek, *Suksdorf* 11664 (WS); "Zahnberg," *Suksdorf*, July 8, 1896 (WS); Chenowith, *Suksdorf* 2568 (WS). Yakima County: North of Wenas, *Thompson* 14556, in part (WS).

2d. LUPINUS ARBUSTUS subsp. SILVICOLA (Heller) Dunn, Leaflet. West. Bot. 7:255. 1955. *Lupinus silvicola* Heller, *Muhlenbergia* 6:81. 1910. Type. Placer County, California, near the summit, *A. A. Heller* 9857 (Nevada Agri. Exp. Sta.; isotypes MO, POM, MIN, NMC, WS, US). *Lu-*

*pinus laxiflorus* var. *silvicola* (Heller) C. P. Smith, in Jeps. Man. Fl. Pl. Calif. 527. 1925. *Lupinus lassenensis* Eastw. Leafl. West. Bot. 4:221. 1946. Type. Manzanita Creek, Lassen Volcanic National Park, California, L. S. Rose 45262 (CAS). *Lupinus laxiflorus* var. *laxiflorus sensu* Phillips *pro parte*, Res. St. State Col. Wash. 23:197. 1955.

Plants 4.5–5 dm. tall, with several stems from a woody caudex, the stems minutely appressed-pubescent to puberulent throughout; leaves cauline with the petioles gradated, 10 cm. long below and 3–4 cm. long above; leaflets 8–10, linear-elliptic, puberulent on both sides, bright green, obtuse or acute, mucronate; peduncles 2–4 cm. long; racemes 8–10 cm. long, flowers scattered or subverticils 8–15 mm. distant; bracts tardily deciduous; pedicels slender, 2–5 mm. long; flowers 6.5–10 mm. long; upper lip of the calyx 3–5 mm. long, the spur ca. 1 mm. long, the tip usually covered by the sides of the banner; banner pubescent dorsally and in the ventral sulcus; wings pubescent laterally near the tip; keel villous-ciliate near the acumen; ovules 4–5; pods 20–25 mm. long, 6–7 mm. wide, finely sericeous.

*Lupinus arbustus* subsp. *silvicola* is centered in the northern Sierra Nevada of California, extending into the Cascade Range of Oregon. It is most commonly found from the arid transition zone, with yellow pine, into the upper Canadian zone, with spruce and white pine. Occasional specimens have been collected at lower elevations. This taxon grades into var. *montanus* in the north and subsp. *calcaratus* along the Sierra Nevada. Gene flow from subsp. *silvicola* was probably responsible for the blue-flowered specimens of subsp. *calcaratus* in northeastern California, which Eastwood called *L. elegantulus*, since these specimens resemble subsp. *silvicola* in being less hairy, but they have the flower proportions of subsp. *calcaratus*. Several of the specimens cited under var. *montanus* from the Mt. Hood area (Martin 4815; Oswego, Millard; Oswego, Drake & Dickson) show characters which suggest gene flow from subsp. *silvicola*. Christ 16868, cited below from Deschutes County, Oregon, is closer to the typical subsp. *silvicola*, but shows traits of var. *montanus*.

Distribution (partial citation). CALIFORNIA. Alpine County: Winnemucca Lake, Woods Lake region, Peirson 12799 (RSA); Lake Alpine region, Peirson 11579 (RSA). Butte County: Jonesville, Copeland 421 (LA, POM, RSA, MO). Eldorado County: trail to upper Echo Lake, Peirson 6309 (RSA). Lassen County: west of Fredonyer Pass, Heller 15142 (RSA, POM, MO). Mariposa County: Inspiration Point, Yosemite, June 5, 1897, Congdon (MIN). Modoc County: Fandango Pass, Warner Mountains, Eastwood & Howell 8141 (CAS). Nevada County: Castle Peak, Howell 18531 (RSA); Donner Lake, Heller 6944 (POM, MIN, MO); Independence Lake, Hall & Babcock 4532 (POM); Soda Springs, M. E. Jones 2406 (POM); Truckee, July, 1895, C. F. Sonne (POM). Placer County: Deepark, Lake Tahoe region, Eastwood 405 (RSA, MO); Summit, Heller 9857 (see type citation). Plumas County: Eureka Peak, J. T. Howell 27699 (RSA); Warner Valley, Applegate 5781 (RSA); Silver Lake, July 13, 1929, Merrill (WS, MO). Shasta County: slope of Diamond Peak, Dunn 11812 (RSA, LA & MIN); Lassen Peak, M. E. Jones 11658 (POM); trail, Drakesbad to summit of Lassen Peak, Peirson 6815 (RSA); two miles east of Hatchet Summit, Heller 15688 (WS, MO). Sierra County: between Gold Lake and Blaisden, Barker 766 (RSA). Siskiyou County: east of Deer Mountain, Heller 15260 (RSA, MO). Tehama

County: Mineral, July 16, 1935, *Epling & Robison* (LA); two miles east of Chico Creek, Highway 32, *Heller 15672* (WS, MO).

OREGON. County ? : Woodville, *T. Howell 1341* (MO). Crook County: mouth of Canyon Creek, Ochoco National Forest, *Kucera 19, 22* (WS); Tumale Ditch, *Whited 624* (WS). Deschutes County: Santiam Pass northeast of Sisters, *Christ 16868* (NY). Klamath County: near Fort Klamath, *Applegate 4096* (RSA, WS). Wasco County: Marion's Point Lookout, Mount Hood National Forest, *G. N. Jones 4028* (POM).

2e. *LUPINUS ARBUSTUS* subsp. *CALCARATUS* (Kell.) Dunn. Leaf. West. Bot. 7:255. 1955. *Lupinus calcaratus* Kell. Proc. Calif. Acad. Sci. 2:195, f. 60. 1862. The illustration becomes the type since the type was lost in the San Francisco fire (International Code, 1952, Art. 21). Type locality not given but probably western Nevada or adjacent California, specimens distributed by P. Train from Convict Creek, Mono County, California, May 30, 1937, may be considered as typical. *Lupinus variegatus* Heller, *Muhlenbergia* 8:89. 1912. Type. Ruby Mountains near Deeth, Elko County, Nevada, *Heller 10551* (Nevada Agri. Exp. Sta.; isotypes, POM, MIN, NMC). *Lupinus multinctus* A. Nels. Bot. Gaz. 53:221. 1912. Type. Big Willow Canyon, Idaho, *J. F. Macbride 114* (isotypes MIN, WS, MO). *Lupinus laxiflorus* var. *calcaratus* (Kell.) C. P. Smith, Bull. Torrey Club 51:304. 1924. *Lupinus laxiflorus* var. *villosulus* C. P. Smith, Am. Jour. Bot. 13:530. 1926. Type. Clove Mountains near Deeth, Nevada, *Heller 9098* (DS). *Lupinus elegantulus* Eastw. Leaf. West. Bot. 3:20. 1941 (an intermediate with subsp. *silvicola*). Type. Fandango Pass, Warner Mountains, Modoc County, California, *Eastwood & Howell 8141* (CAS). *Lupinus noldekeae* Eastw. Leaf. West. Bot. 4:149. 1945. Type. Near Hot Creek, Mono County, California, July 1938, *A. Noldeke* (CAS). *Lupinus geraniophilus* C. P. Smith, Sp. Lup. 727. 1952. Type. Johnson Creek Ranger Station, Weiser National Forest, Idaho, *H. J. Helm 30* (USFS 44172). *Lupinus varneranus* C. P. Smith, Sp. Lup. 730. 1952 (an intermediate with *L. argenteus* var. *tenellus*). Type. Boulder Lake, Idaho National Forest, Idaho, *I. M. Varner 82* (USFS 17912). *Lupinus multinctus* var. *grandjeani* C. P. Smith, Sp. Lup. 735. 1952. Type. Boise National Forest, Elmore County, Idaho, *E. Grandjean 460* (USFS 27399). *Lupinus graciliflorus* C. P. Smith, Sp. Lup. 739. 1952. Type. Fairview Ranger Station, Lemhi National Forest, Idaho, *G. A. Miller M-86* (USFS 63045). *Lupinus laxiflorus* var. *laxiflorus sensu* Phillips *pro parte*, Res. St. State Col. Wash. 23:197. 1955.

Plants generally 4–6 dm. tall with a cluster of stems from a woody caudex, branching above after the primary raceme reaches anthesis, puberulent to finely sericeous and occasionally strigose to somewhat villous; leaves all cauline, the lower petioles up to 15 cm. long, gradated to 2 cm. long above; leaflets 8–10, linear-elliptic-oblancoate, pubescent on both sides, the largest 3–6 cm. long and 4–8 mm. wide; peduncles 2–3 cm. long; racemes 5–10 cm. long, rather dense, the flowers scattered or verticillate, the verticils 8–10 mm. distant; bracts subpersistent to caducous; pedicels 3–4 mm. long; flowers 11–14 mm. long excluding the spur; upper lip of the calyx 6–7 mm. long, including the spur of 1.6–3 mm. in length,

the lower lip 5.5–6.5 mm. long; banner with abundant pubescence on the back or sparsely ciliate in the dorsal grooves, rarely glabrous, also pubescent in the ventral sulcus; wings pubescent laterally near the tip, keel ciliate toward the acumen; ovules 5–6; pods 25–35 mm. long, 8–10 mm. wide, villous.

The subsp. *calcaratus* occupies the mountains of the northern Great Basin, commonly in the *Artemisia* and *Juniperus* belt, but some intermediates are known to extend up into the spruce zone. The blue and lavender forms grade into subspecies *arbusus* var. *montanus*. The flowers of subsp. *calcaratus* are more slender and the calyx spurs longer than those of subsp. *arbusus* var. *montanus*. The upper lip of the calyx may be exposed or partially hidden by the banner. In its typical yellow-white form, it is quite distinct. There also appears to be gene flow between subsp. *calcaratus* and subsp. *silvicola* in the Sierra Nevada of California. The effects of introgression are also apparent between subsp. *calcaratus* and subsp. *pseudoparviflorus* in Idaho.

Distribution (partial citation). CALIFORNIA. Alpine County: Leviathan Creek, *J. C. Johnson* 121 (WS). Inyo County: (w)<sup>1</sup> Andrews Camp, Bishop region, *Peirson* 529 (RSA). Lassen County: (b) 14 miles west of Madeline, *Balls* 14788 (RSA). Modoc County: (b) *Austin & Bruce* 2146 (POM); (lav) Canby Bridge, *Balls* 14742 (RSA); (b) Cedar Pass, *Heller* 16205 (RSA); (w) below Clear Lake, *Balls* 14798 (RSA). Mono County: (w) Convict Lake, *Woglum* 1875 (RSA), May 30, 1937, *Train* (UMO); (lav-w) Sonora Pass, *A. L. Grant* 348, 159, 313 (POM, MO); (w) Long Valley, *Fendge* 1496 (POM); Virginia Lakes Basin, *Peirson* 11215 (RSA); Hot Creek region, *Peirson* 12439 (RSA). Plumas County: (lav) five miles north Chilcoot, *Munz* 11822 (RSA). Tuolumne County: (b-lav) Sonora Pass, *Wiggins* 8127 (RSA).

IDAHO. Ada County: (w) Boise, *Clark* 13 (POM, WS); Owyhee, *M. E. Jones* 25464 (LA). Blaine County: (lav-w) Galena Summit, *Macbride* 3719 (POM, WS, MO). BOISE COUNTY: (yel-w) Squaw Creek (Sweet), *Macbride* 844 (POM, WS, MO). Custer County: (an intermediate with *L. leucophyllus*) 5 miles west of Basin-gers, Little Lost River Valley, *Hitchcock* 15729 (RSA); (lav-w) Malkay, *Nelson & Macbride* 1530 (POM, WS, MO). Elmore County: 15 miles north of Mountain Home, *Hitchcock & Muhlick* 8670 (WS, MO); 3 miles east of Featherville, *Hitchcock* 8780 (WS, MO). Twin Falls County: southeast of Hollister, *Piemeisel* 44, 1032 (RSA). Washington County: Weiser, *M. E. Jones*, July 7, 1899. (POM, MO).

NEVADA. Douglas County: (lav-w) Glenbrook, *Smith* 3803 (POM); Kingsbury Grade to Lake Tahoe, *Train* 3161 (RSA); (lav-w) Spooner, *Smith* 3808 (POM), (lav-b) June 23, 1902, *Baker* (POM). Elko County: 6 miles east of Wells, *Train* 3639 (RSA); near Deeth, *Heller* 9098 (UC); Ruby Mountains near Deeth, *Heller* 10550, 10551 (POM, MIN, Nevada Agri. Exp. Sta.). Esmeralda County: Emigrant Pass, Victory Highway, *Eastwood & Howell* 231 (RSA). Ormsby County: (lav-w) Kings Canyon, *Baker* 923 (POM, MO); (w) Snow Valley Mountains, *Smith* 3837 (POM). Washoe County: Alum Creek, *Heller* 9744 (WS); 2.5 miles northeast of Mount Rose Pass, *Martin* 5539 (RSA, MO); (w) Franktown, *Jones* 3812 (POM), 3815 (MO); (w) Kennedy Pass, Mount Rose, *Heller* 10342 (POM, WS, MO).

OREGON. Baker County: north of Robbinette, *Cronquist* 6524 (WS). Harney County: Andrews, *Applegate* 5635 (WS). Malheur County: 10 miles east of Ironside, *Peck* 26065 (WS); Jamieson, *Peck* 26059 (WS). Sherman County: DeMoss, *Hill* 12

<sup>1</sup> The letters in parentheses at the beginning of each citation refer to the color of the flowers of the specimen: (w)=white. (b)=blue. (lav)=lavender. (yel)=yellow.

(WS), 43175 (WS). Cassia County: 23 miles east of Rogerson, *Christ 18496* (NY). part, *Cusick 1896* (POM, WS, MO); (lav) Lower Powder River, *Cusick 2514* (POM, WS, MO). Wheeler County: 15 miles northeast of Mitchell, *Cronquist 6977* (RSA); John Day River, 1 mile south of Service Creek, between Fossil & Mitchell, *Cronquist 6304* (RSA, WS).

UTAH. Tooele County: (w) Mount Ibapah, *M. E. Jones 11662* (POM, MO), *Jones*, June 23, 1891 (POM).

2f. *LUPINUS ARBUSTUS* subsp. *PSEUDOPARVIFLORUS* (Rydb.) Dunn, Leaflet. West. Bot. 7:255. 1955. *Lupinus pseudoparviflorus* Rydb. Mem. N. Y. Bot. Gard. 1:232. 1900. Type. Bridger Mountains, Montana, *Rydb. & Bessey 4441* (NY; isotypes MIN, WS). *Lupinus laxiflorus* var. *pseudoparviflorus* (Rydb.) C. P. Sm. & St. John in St. John, Fl. S. E. Wash. 227. 1937. *Lupinus laxispicatus* Rydb. Bull. Torrey Club 34:42. 1907. Type. High mountains of Kootenai County, Idaho, *J. H. Sandberg*, July, 1887 (NY). *Lupinus laxiflorus* var. *durabilis* C. P. Smith, Journ. Bot. 13:529. 1926. Type. Bonner County, Idaho, Priest River Range, *J. B. Lieberg 2731* (isotype, US). *Lupinus laxispicatus* var. *whithamii* C. P. Smith in St. John, Fl. S. E. Wash. 227. 1937. Type. Junction of Divide and King Creek trails, Kaniksu National Forest, Washington, *C. P. Smith, St. John & Whitham 4170* (DS-Sm; isotype and paratypes at WS). *Lupinus sulphureus* subsp. *whithamii* (C. P. Smith) Phillips, Res. St. State Col. Wash. 23:193. 1955. *Lupinus laxiflorus* var. *elmerianus* C. P. Smith, Sp. Lup. 106. 1939. Type. Paradise, Wallowa County, Oregon, *E. I. Applegate 6483* (DS). *Lupinus mucronulatus* var. *umatillensis* C. P. Smith, Sp. Lup. 108. 1939. Type. Table Rock, Umatilla County, Oregon, July, 1930, *Eldon W. Lyle* (DS). *Lupinus fieldianus* C. P. Smith, Sp. Lup. 567. 1946 (an intermediate with subsp. *neolaxiflorus* Dunn). Type. Thorn Creek, Idaho National Forest, Idaho, *R. C. Fields 224* (USFS 23418). *Lupinus lacus-payetti* C. P. Smith, Sp. Lup. 574. 1946. Type. Payette Lake, Idaho, *M. E. Jones 6251* (POM, MO, US).

Plants 3–6 dm. tall, with several simple stems from a woody caudex, these branching later from the upper nodes, the stems 1.5–2.5 mm. in diameter, finely, thinly sericeous, with basal leaves generally present at anthesis; petioles of the basal leaves 8.5–15 cm. long, those of the upper cauline leaves 2.5–3 cm. long; leaflets 7–11, the largest 4–6 (–8) cm. long and 6–10 mm. wide, the tips rounded, or obtuse to acute in intermediate forms; leaflets commonly glabrous on the upper surface, the intermediate forms sparsely pubescent; peduncles 3–6 cm. long; racemes 3–12 cm. long, lax or dense; bracts caducous or tardily deciduous; flowers 9.5–13 mm. long; pedicels 3–5 mm. long, sometimes up to 10 mm. long; upper lip of the calyx gibbous or with a spur 0.6–1.4 mm. long, the tip usually covered by the sides of the banner; banner finely pubescent in the central area or glabrous in 10–30 per cent of the specimens; the wings glabrous in about 30 per cent of the specimens, the others pubescent near the tip; the keel ciliate above near the acumen, sometimes glabrous; pods 7.5–9 mm. wide, 25–35 mm. long, villous, with 3–6 ovules.

*Lupinus arbustus* subsp. *pseudoparviflorus* is found in relatively moist habitats but with some drainage, often in considerable shade, from the Douglas fir or lodge-pole pine zones on up to the aspen, spruce and white-pine zones. The center of distribution is in the mountains of western Montana and northern Idaho and southward into Colorado. The occasional plants in the mountains of southern Idaho and the one collection from northeastern Nevada may be thought of as relictual populations.

The material treated here as subsp. *pseudoparviflorus* is somewhat heterogeneous, and breeding studies may reveal that some of the taxa cited as synonyms may require recognition. Smith's var. *elmerianus* is intermediate to subsp. *arbustus* var. *montanus*, having the acute leaflet tips of that variety and a vegetative habit which approaches it, but having glabrate upper leaf surfaces. The two specimens of *L. scheuberae* Rydb. which were seen resemble subsp. *pseudoparviflorus* and have been included in the synonymy of *pseudoparviflorus* by authors, but the flower size of 14 mm. and the vegetative characters suggest to me that *L. scheuberae* may have resulted from hybridization between *L. burkei* S. Wats. and subsp. *pseudoparviflorus*. I have not included *L. scheuberae* here as a synonym of the latter taxon since the morphological hiatus suggests it may warrant treatment as a named hybrid. There is also a race of subsp. *pseudoparviflorus* present in the Bitterroot Valley, Missoula, Montana, which is one of the more distinctive segregates. This race has the narrowest leaflets, racemes up to 25 cm. long, pedicels to 10 mm. long, and becomes 7-9 dm. tall. It has not been named, but it is far more distinctive than most of the variants that have names. It seems best at present merely to call attention to the fact that these plants form what appears to be a morphological extreme within the range of variation attributed to *pseudoparviflorus*.

The var. *whithamii* C. P. Smith may warrant recognition, but the "glabrous wings" which characterize this variety occurred in a high percentage of the specimens in subsp. *neolaxiflorus*, as well as in a fair percentage of the rest of the population of subsp. *pseudoparviflorus*. The highest percentage of individuals that were glabrous in one or more of the flower parts occurred in the population in northern Idaho and Washington. The glabrous nature was observed again in the specimens from Colorado, but there it appears to be due to introgression from *L. rubricaulis* of the *L. argenteus* complex.

Distribution (partial citation). COLORADO. Larimer County: near North Park, Aug., 1894, *Osterhaut* (PHIL). County?: Ursten's Pass, July, 1873, *Coulter* (PHIL).

IDAHO. Bonner County: Priest River, Experimental Forest, *Daubenmire* 43122 (WS), 43175 (WS). Cassia County: 23 miles east of Rogerson, *Christ* 18496 (NY). Bear Lake County: 13 miles west of Bloomington, *Christ* 18678 (NY). Clearwater County: above Orofino, *Constance*, *Dimond*, *Rollins* & *Worley* 1082 (WS). Idaho County: Indian Post Office, *Q. Jones* 293 (RSA); 5 miles south of Harpster, cliffs above Clearwater River, *Hitchcock* & *Muhlick* 8452 (WS). Latah County: 8 miles south of Troy, *Daubenmire* 46131 (WS); Paradise Ridge, *Daubenmire* 37403 (approaches *L. scheuberae*) (WS). Lemhi County: 6 miles north of Gibbonville, Salmon

River, *Christ & Ward 14695* (NY); Panther Creek 8 miles north of Cabin Creek, *Hitchcock 14270* (POM, RSA). Lewis County: Mission Creek, *St. John, Cary, Putnam & Warren 3247* (WS); north edge of Winchester, *Daubenmire 46237* (WS). Nez Perce County: near Lewiston, *Heller 3224* (WS, MO); bluffs of Clearwater River north of Spalding, *Daubenmire 37479* (WS). Shoshone County: Siwash Peak, St. Joe National Forest, *Moore 433* (WS); sides of Quarles Peak, *Wilson 193, 211, 205*, the latter approaching *L. scheuberae* (WS).

MONTANA. Flathead County: southeast of McDonald Lake, *Hitchcock 18280* (RSA, WS); Columbia Falls, *Dunn 9723* (RSA, LA, MIN, UMO), June, 1894, *Williams* (UMO). Gallatin County: Bridger Mountains, 1 mile south of Brackett Creek, *Hitchcock & Muhlick 12460* (WS, MO); Middle Creek Canyon, Bozeman, *Blankinship*, June 26, 1900 (WS). Lake County: 10 miles northeast Polson, Flathead Lake shore, *Hitchcock 15344* (RSA, WS). Lewis & Clark County: 3 miles east of Danaher Ranger Station, *Hitchcock 18718* (RSA, WS). Missoula County: Bitterroot Valley, *M. E. Jones 11655* (POM); Rattlesnake Drainage, *Hitchcock 14560* (RSA, WS). Park County: 15 miles south of Wilsall, *Hitchcock & Muhlick 12438* (WS). Powell County: 8 miles northeast of Helmville, *Hitchcock 17843* (RSA, WS). Ravalli County: Palisade Pl. Ranger Station, Bitterroot Mountains, *Hitchcock 15344* (RSA). Sanders County: 3 miles west of Dixon, *Hitchcock 2873* (WS). County?: Nanicke, *Cooke 17324* (WS).

OREGON. Wallowa County: Paradise, *Applegate 6483*; east of Sacajawea Camp over the Snake River Canyon, *Kruckeberg 2456* (RSA, WS).

WASHINGTON. Chelan County: Mission Canyon, 10 miles south of Cashmere, *Hitchcock 17304* (WS); 15–20 miles up Wenatchee River, near Cascade Mountains, 1889, *Vasey 38752* (WS). Okanogan County: head of Cedar Creek, south of Conconully, *Fiker 831, 832, 883* (WS). Pend Oreille County: divide & Kings trail, junction, Kaniksu National Forest, *Smith, St. John & Whitham 4171, 4177* (WS); Kings Lake Road, below south Skookum Drive, Kaniksu National Forest, *Smith, St. John & Whitham 4169, 4180* (WS). Spokane County: Newman Lake, *Smith & St. John 4135, 4136* (WS).

University of Missouri,  
Columbia, Missouri.

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## SOME ADDITIONS TO THE CALIFORNIA MOSS FLORA

HOWARD CRUM<sup>1</sup>

Considerable work has been done on the moss flora of California during recent years, and a firm basis has been laid for further floristic studies by the publication of a checklist of California mosses by Koch (1950). The size of the state and the extreme diversity of available habitats make it probable, however, that many more species will be discovered in California, not only by careful collecting but also by critical study of many difficult genera, particularly of the Pottiaceae and the Brachytheciaceae. Recently, from 1954 to 1956, Wilfred B. Schofield of Wolfville, Nova Scotia, made a sizable and very interesting collection of mosses in central California, mostly in the San Francisco Bay region. In addition to many rarities previously recorded from the area, he found one very distinctive new species and several important range extensions which are reported below. A few additional specimens worthy of recording here were sent me for determination or confirmation by Mrs. Fay A. MacFadden of Los Angeles. All the specimens are deposited in the Herbarium of the National Museum of Canada (CAN).

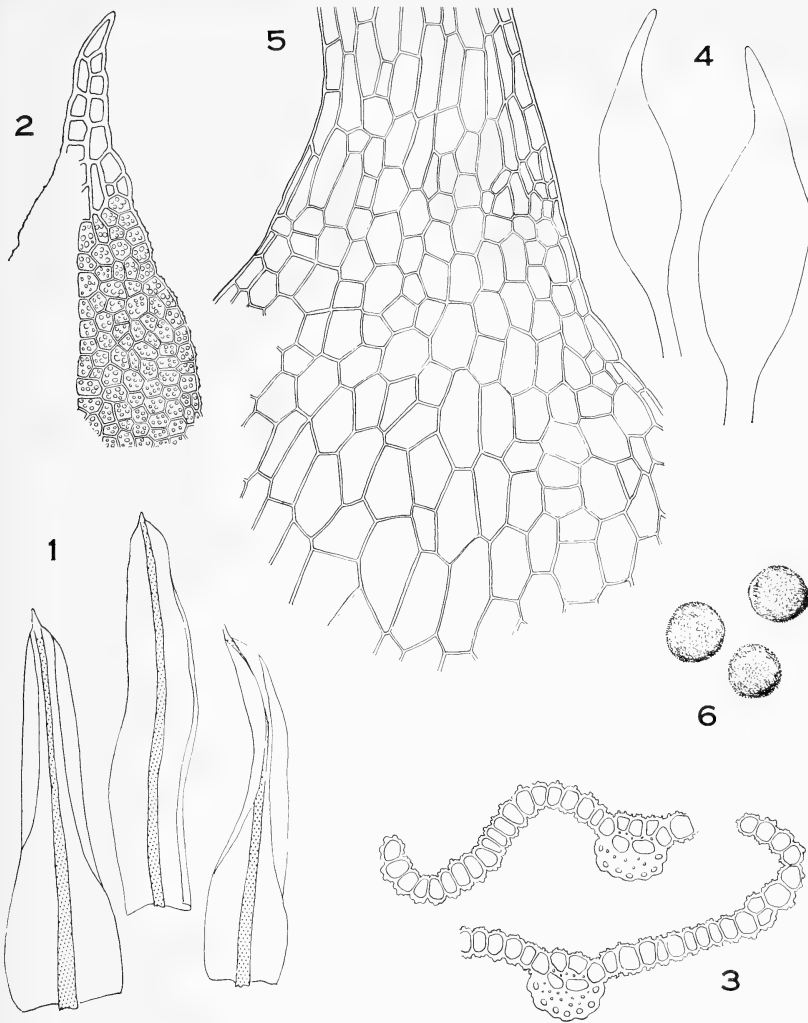
**Hymenostomum** (Kleioweisia) **inoperculatum** sp. nov. (Figs. 1-6). Planta tenella, usque ad 1 mm., sordido-viridis, paucifolius, folia usque ad 2 mm. longa, madida patula, sicca crispula, inferiora minuta et ovata, caetera sensim major, oblongo-lanceolata, acuta et apiculata, concava, marginibus integerrimis, superne late involutis; costa basi 48-56 $\mu$ , breviter excurrens; cellulae basilares in dimidio inferiore hyalinae, oblongae, parietibus tenuibus, cellulae laminae superioris hexagonae, opacae, densissime papillosoe, dioicum (?); flos masculuae non vidi, seta 3 mm. longa, pallida, erecta; capsula 1.25-1.75 mm. longa, exserta, erecta, oblongo-cylindrica, oblique et longe rostrata, clausa, sine operculo, sporae 16-19 $\mu$ , minute et dense papillosoe.

Type. On soil in garden in front of Sequoia Hall, Stanford University, Santa Clara County, California, February, 1955, *W. B. Schofield (s.n.)*; growing with *Pottia arizonica* var. *mucronulata* Wareham (CAN).

This species is distinct from all other American species of *Hymenostomum* known to me in having clearly exserted, cleistocarpous capsules. It is related, perhaps most closely, to *H. exsertum* (Broth.) Broth. of China and Japan, but judging from the single Japanese specimen which I have seen, named by Dr. Akira Noguchi and kindly communicated by Dr. Harumi Ochi, the Californian species differs markedly in having much shorter and relatively broader leaves which are less strongly crisped when dry and capsules which are narrower and cylindric to subelliptic, rather than subglobose, and end in longer, more slender beaks. A further difference is that the capsules are clearly exserted, and the setae much exceed the uppermost leaves in length, whereas in *H. exsertum*, although the

<sup>1</sup> Published by permission of the Director of the National Museum of Canada, Ottawa.





FIGS. 1-6. *Hymenostomum inoperculatum*. 1, leaves,  $\times 30$ ; 2, upper cells of leaf and apiculus,  $\times 275$ ; 3, two sections taken in upper portion of leaf,  $\times 275$ ; 4, two capsules,  $\times 30$ ; 5, areolation of capsule wall showing the irregularity of cells at the zone of dehiscence in most other species of mosses,  $\times 275$ ; 6, spores,  $\times 520$ .

setae are fairly long and the capsules appear to be exserted, they are actually surpassed in length by the strongly contorted and spreading upper leaves. *Hymenostomum inoperculatum* conforms very well to the description of *H. semidiaphanum* Thér. of Mexico, but the type of that species was examined and found to be inaccurately characterized. The operculum is clearly differentiated and not "haud secedens." (Thériot was probably

misled by the juvenile development of the capsules in the type collection of *H. semidiaphanum*.) The position of *H. semidiaphanum* in the subgenus *Kleioweisia* seems highly unlikely.

*POTTIA ARIZONICA* var. *MUCRONULATA* Wareham. On soil in garden in front of Sequoia Hall, Stanford University, Santa Clara County, February, 1955, *W. B. Schofield* (s.n.). I have examined the only previous California collection, from Los Angeles County (Koch, 1950), as well as the type from Arizona.

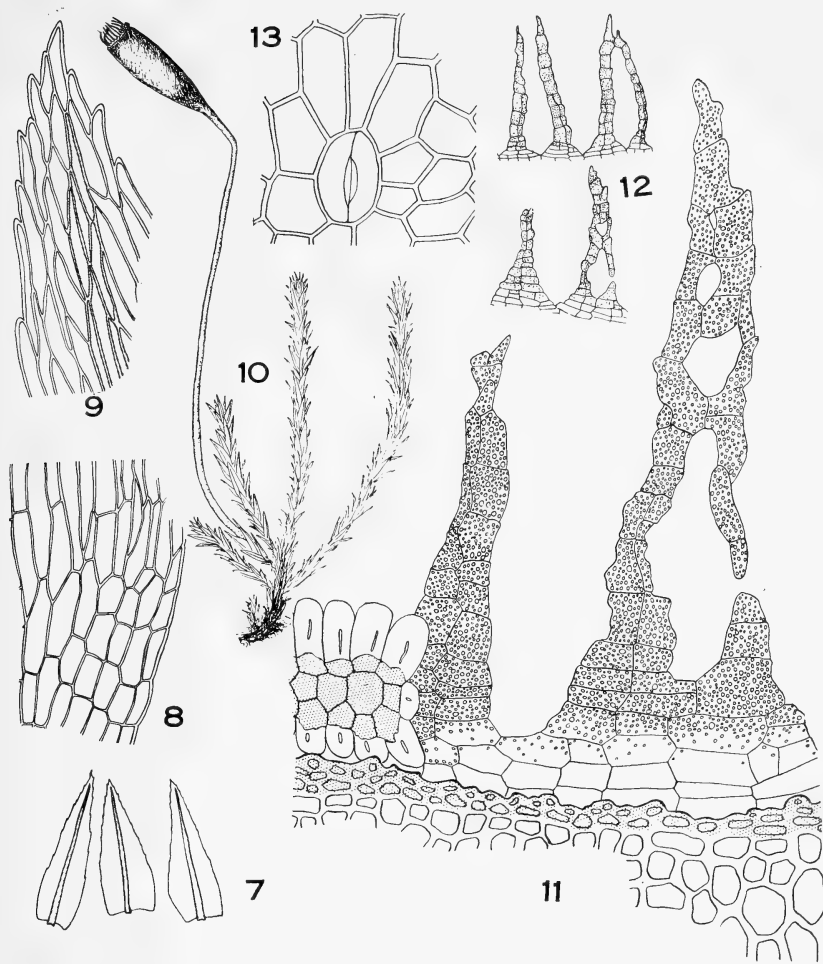
*STEGONIA LATIFOLIA* var. *PILIFERA* (Brid.) Broth. This interesting moss, previously known only from the Yukon and from the Canadian Rocky Mountains in North America, was collected among rocks at 13,950 feet altitude on Mount Barnard, Tulare County, by Peter H. Raven on July 25, 1955. The specimen was sent me by Mrs. MacFadden.

*TORTULA STANFORDENSIS* Steere. On moist, hard-packed soil of open area, Purissima Creek, San Mateo County, November 8, 1955, *W. B. Schofield* 6322. This species, recently described from Santa Clara County (Steere, 1951), has also been reported from Alameda County (Koch & Ikenberry, 1954).

*GRIMMIA MARINIANA* Sayre. Dark, hyaline-tipped cushions among boulder crevices, Mount Tamalpais, Marin County, March 26, 1955, *W. B. Schofield* 5798; steep, exposed rocks, east side of East Peak, Mount Tamalpais, Marin County, April 8, 1956, *John T. Howell* H184 (comm. Mrs. MacFadden). Both of these specimens come from the general vicinity of the type locality and conform very well to Sayre's recent description (1955), except that the alar cells of the leaves have thickened cross-walls, a character which Sayre perhaps overlooked.

*EPEMERUM MINUTISSIMUM* Lindb. Locally abundant on small, clayey patches in an open field, Big Basin, Santa Cruz County, March 24, 1956, *W. B. Schofield* 6450; local, on bare patches near margin of field, near Ventura Hall, Stanford University, Santa Clara County, February 23, 1955, *W. B. Schofield* 5723. Duplicates of these specimens were sent to Dr. Virginia S. Bryan, who confirmed the determinations tentatively, pending further understanding of the puzzling variation exhibited by *E. serratum* and *E. minutissimum* in the West. Koch (1950) listed only *E. serratum* (Hedw.) Hampe from California, where it had been collected only once, in San Francisco. Grout (1928-40) mentioned only Massachusetts and Saskatchewan in the distribution of *E. minutissimum*.

*MIELICHHOFERIA MIELICHHOFERIANA* (Funck) Limpr. (figs. 7-13). On a tree trunk, Little Butano Creek, Santa Clara County, November 6, 1954, *W. B. Schofield* 5748. Extremely rare and localized in its distribution, this species has been collected in only a few other widely separated places in North America (in the Lake Superior region of Michigan and Ontario and also in Maine). In the Old World it is known from Scandinavia, the Alps and elsewhere in Central Europe, the Pyrenees, and the Caucasus. The plants which Mr. Schofield collected in the Coast Ranges



FIGS. 7-13. *Mielichhoferia mielichhoferiana*. 7, leaves,  $\times 23$ ; 8, basal cells of leaf,  $\times 205$ ; 9, upper cells of leaf,  $\times 205$ ; 10, habit of fruiting plant,  $\times 8$ ; 11, portion of peristome, annulus, and upper exothecial region,  $\times 205$ ; 12, portions of peristomes, showing variation in shape of teeth,  $\times 65$ ; 13, cells from neck of capsule showing stoma,  $\times 205$ .

of central California seem to me typical in every structural detail and only slightly different in habit of growth, as they are somewhat more elongate, less densely compacted in tufts and more loosely and freely branched than any other material that I have examined, although they greatly resemble in growth form the illustrations given in the "Bryologia Europaea" (plate 328, as *M. nitida* Hornsch.) and reproduced in Grout's "Moss Flora of North America." These differences are indeed slight and almost

surely not of a genetic nature, and they are doubtless associated with the unusual habitat in which the plants were found, namely, on the bark of a tree. Insofar as I have been able to ascertain, the species has never before been reported from any substrate other than rock and, more specifically, from rocks containing alum or iron and copper ions. Persson (1948) has recently reviewed the evidence for believing that the genus *Mielichhoferia* shows a predilection for copper-containing rocks.

More typically developed, though sterile, plants of a *Mielichhoferia*, tentatively named *M. mielichhoferiana* by A. LeRoy Andrews, were also collected in California by John Thomas Howell "on shaded, moist rock, Merced River Canyon, just above Briceburg, Mariposa County." They were recently sent to me by Mrs. MacFadden, and I see no reason to doubt the determination.

I have prepared the accompanying camera lucida drawings in order to give greater publicity to *M. mielichhoferiana*, as this interesting and rarely collected species has not been illustrated from American material before. It should be noted that the shape of the capsule varies with age. When old, empty and somewhat wrinkled, it is oblong-cylindric, but when operculate, it is more ovoid with a more distinct neck.

*ZYGODON VIRIDISSIMUS* (Dicks.) Brown. In crevices of bark of *Lithocarpus*, forming small patches, Big Basin, Santa Cruz County, November 27, 1955, *W. B. Schofield* 6371. Subsequent to the publication of his checklist, Koch (1950a) reported this species for the first time from California, from a collection made in Humboldt County.

*BRACHYTHECIUM WASHINGTONIANUM* Eaton ex Grout. On shaded soil bank, Purissima Creek, San Mateo County, November 8, 1956, *W. B. Schofield* 6337; on wet bank, same locality and date, 6346; rock outcropping of brook bank, Big Basin, Santa Cruz County, November 27, 1955, *W. B. Schofield* 6357. Koch (1950) listed three collections of this species from Trinity, Siskiyou, and Humboldt counties. These collections extend the range southward considerably. I have studied the type, which comes from Washington. The alar cells of the stem leaves are large and lax and much more clearly differentiated than Grout (1928-40) indicated and seem to me indicative of a clearer relationship to *B. rivulare* B.S.G. than Grout appears to have realized.

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## REVIEW

*The Genus Nicotiana*. By T. H. GOODSPEED. xxi + 536 pp., illustrated. *Chronica Botanica* Vol. 16, No. 1/6. 1954. Waltham, Mass.: The Chronica Botanica Co.; San Francisco, Calif.: J. W. Stacey, Inc. Buckram. \$12.50.

According to Professor Goodspeed: "The primary objective of the *Nicotiana* investigations . . . has been the accumulation of evidence bearing upon the origin, evolution and relationships of the modern species of the genus (p. 1)." Merely as a general presentation of this accumulated information this book is impressive. As Volume 16 of *Chronica Botanica*, it contains some 536 pages, 50 tables, and 118 plates as well as text-figures. Studies in distribution, morphology, and cytogenetics (comprising the first four parts of the book), many of which began as long ago as 1904, are discussed in detail. The important contributions of the *Nicotiana* work to general genetics and cytology are not touched upon, however, for obvious reasons. It is very useful, of course, to have all of this material, which has appeared in many different journals over the years, brought together and integrated. One cannot fail to be impressed with the Olympian outlook of the author as he discusses a genus which has contributed so much to an understanding of basic biological problems. One must always keep in mind, however, that, in a summary work of this sort, there is a great deal more interpretation, or even opinion, than in the individual contributions.

Part I is concerned with the evidence from distribution. Since there is no paleobotanical evidence to use in determining past distribution, Goodspeed discusses in detail the present distribution upon the major land masses. Much of this is repetitive from chapter to chapter and speculative, and suffers from the defects of reasoning based upon patterns of distribution. It may be true that in paleontology one must assume that the present is the key to the past. But when one is dealing with patterns of geographical occurrence he never has all of the requisite facts of present-day ecology and genetics to make an adequate judgment of the factors involved in the past. Nevertheless, Goodspeed deduces that *Nicotiana* originated in South America in the early Tertiary, thence spreading to North America and across Antarctica to Australia, New Zealand, and the islands of the South Pacific. The bases for these deductions appear to be primarily the times at which the various land masses involved became joined or separated and the presumed length of time for a particular "quantity" of evolution to have taken place. The limits of error of these two criteria have scarcely been securely set. But then this is more or less standard operating procedure in taxonomic problems and has been for some time.

All but four of the sixty recognized species of *Nicotiana* have been grown in the greenhouse or field and have been available for experimental studies. Morphological and anatomical investigations have been carried out on all. Goodspeed limits his discussion to general morphology, anatomy, and trichomes (Part II), cytology of species (Part III), and cytology of  $F_1$  interspecific hybrids (Part IV). *Nicotiana* is not characterized by any one specialized feature and there is marked variation between species in habit, inflorescence, and flower, all of which is well illustrated. As one would expect, the majority of anatomical distinctions are quantitative and thus of less use at the level of species. Goodspeed attaches especial importance to the trichomes which are believed to follow patterns paralleling those developed from studies of general morphology, geographical distribution, and cytogenetics.

An especially interesting part of the book for me is the section on the cytology of

species and the cytology of  $F_1$  interspecific hybrids. The details of chromosome morphology and behavior for fifty-six species and their hybrids are described in five chapters. Apparently there is no species known to be an obligate apomict, but some may be facultatively apomictic upon occasion. Chromosome morphology is quite homogeneous. Aneuploidy appears to be rare, but amphiploidy is of frequent occurrence and is thought to be a basic factor in the earliest evolution of the genus. Karyotypes and complete meiotic sequences in representative species and hybrids are illustrated. In the interests of establishing chromosome homology, which is expressed in the amount and type of pairing in  $F_1$  hybrids, Goodspeed makes an analysis of 215 cases. He finds that they may be grouped into five categories ranging from complete pairing to almost no pairing. It is obvious that the analysis of chromosome nature and behavior forms a major source of criteria for the segregation and alignment of groups of species and sections.

Part V, entitled "Phytesis," consists of two chapters. The first paints in very broad and general terms the author's views concerning the origin, relationships, and evolution in the genus. The second discusses the possible "future" of the genus and is based upon what is deduced about the present and the past. Here, as elsewhere in the book, little information is given about the genetics of species populations. One does not gain any concept of population structure or, indeed, of the genetic systems at work at the level of species and below. This is a very noticeable and, I would think, serious gap in the presentation and in the data. Goodspeed envisions the present-day species to have arisen from a complex comprising pre-Nicotiana, pre-Cestrum, and pre-Petunia elements. Evolution of these hypothetical forms presumably gave rise to the modern genus with its cestroid and petunioid complexes. *Nicotiana* can be considered the residue of a polyploid complex based on the chromosome number  $n=6$ . Forms with this number are no longer extant, however, and the existing species may be arranged on two levels of polyploidy with about one-third of these at the higher level. These conclusions are diagrammed in an interesting representation of the levels of advancement and the degree of relationship of the various taxa. Goodspeed believes that in the future: "... the genus may be expected to expand both genetically and geographically, with greatest increase in number of species on the higher polyploid level."

The concluding section of the work, written with the collaboration of Helen-Mar Wheeler and Paul C. Hutchison, is the section on formal taxonomy and nomenclature. Its 170 pages contain the usual historical resumé, generic and specific descriptions, keys to taxa, and lists of cited specimens. Here the relatively minor attention devoted to lower categories is emphasized by the use of variety as the only category below the rank of species and, while these are keyed out, they are not discussed in detail. One cannot be sure whether the authors really mean these forms to be considered taxa below the level of subspecies (as the International Rules of Botanical Nomenclature would indicate) or if they consider the term variety to be equivalent to subspecies or to be the only infraspecific category.

The reader will almost certainly be drawn to make a comparison between "The genus *Nicotiana*" and other general works on genera of plants and animals which have appeared in the last few years. I feel that it is not only difficult, but somewhat unfair, to make such comparisons. Investigators have naturally emphasized those features of the groups upon which they have worked which are the most amenable to study and which thus make a significant quantitative as well as qualitative contribution. For *Nicotiana* it would seem that the greatest contributions lie in the fields of morphology and cytogenetics. For this reason Goodspeed's book will be an indispensable reference work for the biologist interested in evolutionary problems.—RICHARD W. HOLM, Department of Biological Sciences, Stanford University.

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## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madrño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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THE CONCEPT OF THE FLOWER AND THE THEORY OF  
HOMOLOGY<sup>1</sup>

HERBERT L. MASON

In seeking sound concepts around which to build our ideas of the taxonomy of the flowering plants, we find that confidence in our concepts of the flower has steadily deteriorated since the exposition and later clarification of the classical theory of the flower and especially since the publication by Zimmermann (1930) of the telome theory. The ideas embodied in the classical theory—namely, that the parts of the flower are metamorphosed leaves—had their beginnings early in botanical history, going back at least to Linnaeus and several of his associates. The most significant enunciations of the theory, however, are accorded to Caspar Friedrich Wulff (Samassa, 1896) and to the poet-philosopher Wolfgang von Goethe (1790). It is important to realize that the classical theory embodied the concept of homology that was being discussed by the 18th and 19th century anatomical philosophers of Germany and France, including also such men as Cuvier (1800), Oken (1807), and St. Hilaire (1807). The concept originated in the thinking of the classical geometers and was here being applied to biology. The language was vague because its abstractions, although clear to its authors, were burdened with confusions of logical types that led to confusion of understanding among the readers in their attempts to apply it. For instance, Goethe spoke of the parts of the flower as being “metamorphosed leaves” while Oken created bewilderment among zoologists by speaking of the “humerus of the head.” These ideas became variously known in botany as the “classical theory of the flower” or, more broadly, as “the theory of morphology,” alluding here to the concept of homology that was embodied in it. It met with immediate criticism as presenting an illogical consequence, since “that which never was a leaf could scarcely be a metamorphosed leaf.”

There followed a period of great discussion. Of the clarifications which emerged, that expressed by the British botanist, Lindley (1838, p. 59), seems especially worthy of our attention because it constitutes one of the first clear expressions of the concept of morphological equivalence. Said

<sup>1</sup>The substance of this paper was presented to the Eighth International Botanical Congress in Paris in 1954 under the title, “The Controversy of the Flower and its Bearing on Phylogenetic Taxonomy.” Prior to this it was presented in seminars at the Davis and Berkeley campuses of the University of California and at Stanford University. Since these preliminary presentations the manuscript has been amended to indicate the formal nature of the Theory of Homology, and the title has been changed to indicate more precisely the scope of the paper.

Acknowledgments are due to Jean Langenheim for many lively discussions leading to the organization and clarification of the subject matter, and to Annetta Carter, Francia Chisaki, Helen Sharsmith, and Isabelle Tavares for assistance in perfection of the manuscript.

Lindley, "It has been observed in a report made to the British Association at their meeting in Cambridge in 1833, when adverting to this doctrine, that when those who first seized upon the important but neglected facts out of which the modern theory of morphology has been constructed, asserted that all appendages of the axis of the plant are metamorphosed leaves, more was certainly stated than evidence would justify: for we cannot say that an organ is a metamorphosed leaf which in point of fact, never was a leaf. What was meant, and that which is supported by the most conclusive evidence, is, that every appendage of the axis, whether leaf, bract, sepal, petal, stamen or carpel, is originally constructed of the same elements, arranged upon a common plan, and varying in their manner of development, not on account of any original difference of structure, but on account of special and local predisposing causes; of this the leaf is taken as the type because it is the organ which is most usually the result of the development of those elements; is that to which other organs generally revert when, from any accidental disturbing cause, they do not assume the appearance to which they were originally predisposed; and moreover is that in which we have the most complete state of organization."

There are several interesting ideas embodied in Lindley's statement with which we may or may not agree. But what is important to my thesis is the concept of morphological equivalence which assumes that equivalent structures have had a like origin, are arranged in accordance with a common plan, and differ from one another in their further development as a consequence of special and local predisposing causes. This assumes some sort of identity in the early ontogenetic stages. Some such ideas as here expressed have governed the thinking in morphological research for a century and a half. To a large measure they have been responsible for the common practice of interpreting one structure in terms of another on the assumption that all structures are deviations from a prior "common plan." Each structure is assumed to have arisen through the ontogenetic modification of a pre-existing structure. Thus the concepts of the classical theory and of morphological equivalence, at least as to their explanation, are definitely ontogenetic concepts whose explanation rests in knowledge of ontogeny.

The alternative to these ideas is that structures arise anew, possibly upon a foundation of the old, but in no sense to be regarded as being a modification of the old. A structure arising in this manner is said to arise *sui generis*. This idea also has followers, among them Gregoire (1938). I do not imply in placing this theory in apposition to the preceding that it does not also entail an ontogenetic explanation.

As we look into modern concepts of the flower we find that both the classical theory and the concept of homology generally are being seriously questioned as logical bases for morphological interpretation. New approaches to the problem are being investigated outside the scope of the classical theory and the concept of homology. Since a sound taxonomy of

the flowering plants and especially a sound basis for phylogenetic interpretation must rest upon an understanding of the flower, I have attempted to review these concepts and evaluate this controversy in the hope of developing at least an adequate working hypothesis concerning the flower that might prove of value to taxonomy.

As we examine the various theories of the flower that have deviated from the classical theory, nearly all point to the fact that the classical theory fails to explain one aspect or another of the flower. Most workers pointed to various features of the carpel, especially to its relation to structures resulting in an inferior ovary, as not being interpretable in terms of the homologies of appendages. With these difficulties as a beginning, other difficulties became apparent, and there ensued a re-evaluation of all points of difference between carpels and typical leaves and of other parts of the flower in their departure from appendages homologous with leaves. Some workers have investigated the organogenesis of the flower apex in comparison with that of the shoot and have pointed to differences. As a result of their researches upon these problems, Thomas (1934), Thompson (1935), Gregoire (1938), and Lam (1948) insist that an entirely new approach to the interpretation of the flower is called for. In fact Gregoire would overthrow homology as being inapplicable to any comparison of the flower and the shoot, and would insist that the flower is an organ *sui generis* and not in any ontogenetic sense comparable with a shoot. This point is amply discussed and the argument met by Boke (1947).

I do not intend systematically to discuss here the points raised by each of these investigators; what I am concerned with is a re-evaluation of the investigative and intellectual approaches to the problem.

There are at least two basic approaches to the study of the flower. The first of these, the traditional method, employed the concept of homology as a system of logic interpreting structures in terms of abstract categorical levels of morphological equivalence, without necessarily knowing the precise details of ontogenetic elaboration beyond identity, origin, and relative position. This method has been useful, for, although it did no more than categorize structures in terms of the formal relations of a unitary classification, it aided in determining what were comparable structures and at the same time provided a basis, on the one hand, for explaining points of likeness between two structures, and, on the other, a point of departure for ordering and explaining the differences between structures. This has been the chief use to taxonomy of the classical method of morphology.

The other approach to the problem seeks more precise information. It presumes to base its interpretations upon discovering the details of ontogenetic elaboration. Obviously, if such researches are faithfully followed to their conclusion and the details of ontogenetic elaboration carefully worked out, we will have a considerable body of fact upon which to base our judgments and our interpretations, but such facts will in no way eliminate the need of a logical system nor obviate the necessity of establishing intellectual concepts for interpretation.

As we review the controversy of the flower, it appears to be a controversy between these two approaches to the interpretation of the flower. The researches of Zimmermann and his development of the telome theory call for detailed investigation of anatomical organization and ontogeny at a level of structural organization below that envisaged in the system of logic developed by Goethe for the classical theory of the flower, which operated strictly on the level of gross organography. If we are to employ the concept of homology to function at this more detailed level, we will have to redesign our system of logic so that it will be useful in terms of the structures that pertain at this level of organization. To some, the telome serves this purpose (Zimmermann, 1930). The telome is defined in terms of empirical criteria derived from the structure of the extinct Psilophytelean genus *Rhynia* wherein the terminal segment of the axis beyond the last dichotomy is accepted as the basis of the concept of the telome. The segment of the axis upon which the telome rests is called the mesome. Thus telomes, as they give rise to new telomes in their ontogeny, become mesomes. It follows that if we can get at the facts of anatomy, we should be able to trace, through the structure of the individual, the ontogenetic history of telome elaboration, and, through the ontogeny of elaboration of the individual, we may be able to interpret the phylogeny of telome differentiation in the origin of organs. This is the simple logic of the case, and we read such phrases as "seeking the evidence of ancient dichotomies" (Lam, 1948). Obviously the details of morphological differentiation in the higher plants are more complicated than those evident in the fossil *Rhynia*. These complications are systematically explained in the telome theory by a series of elementary processes accounting for the origin of the telome and its phylogenetic elaboration to produce the most complicated of higher plants. I shall not go into this in detail, but will discuss some limitations to its use in comparative morphology. It is sufficient here to call attention to the fact that, like the cell, the telome is thought of as a ubiquitous structure in the plant.

Not all of the discontent with the classical theory emanates from followers of the telome theory. My point is that the wave of reactivated discontent began with the detailed anatomical analysis of structure called into operation by the telome theory and rests primarily upon evidence pertaining to an anatomical level of organization not adequately accounted for in the classical theory of Goethe based on organography.

It should be clear that the telome theory—namely, that plant structures are compounded of telomes in accordance with the operation of the elementary processes—like the classical theory and the principle of homology is a system of logic. As a system of logic it is designed to interpret structures on the basis of criteria significant to telomes and the elementary processes significant to their elaboration. The principle of homology, on the other hand, is a system of logic designed to interpret structures through the logic of comparison resting upon comparable criteria significant to morphological equivalence. The logical consequences of the prin-

ciple of homology are not to be judged by the criteria of the telome theory. These criteria are pertinent only to the logical system for which they were developed. There is nothing inherent in the telome theory that can invalidate either the classical theory or the principle of homology. We, as the designers of these systems of logic, can, if the facts warrant, say that one system explains the situation much better than the other and we may accept or reject on that basis. On the other hand we may alter the system of logic to make it more effective, and, if the altered system proves to be more efficacious, we may replace the old with the new.

Having investigated the problem of the flower both by studying its presentation in the literature and by reviewing the structural features of a large number of different kinds of flowers, I have assessed this controversy as resting primarily in difficulties with our system of logic, in part with our failure to establish adequate diagnostic criteria for the categories into which we would classify the structures of the flower and in part with a confusion of description with ontogeny and phylogeny, rather than with any unusual difficulties inherent in floral anatomy. The chief anatomical difficulty is largely a matter of determining 'when is a structure a new structure?' meaning by this, when does it depart from being an integral part of the structure that bears it? This, I think, can be answered strictly within the framework of the principles of homology, viewing each case, to be sure, in its ontogenetic setting, but primarily viewing each structure for what it is.

In discussing the concept of homology I shall employ a diagrammatic design (fig. 1) which may be spoken of as an organization system (Woodger, 1929). This is strictly a design for displaying an idea, and as I employ it, it is not to be construed as meaningful to any other purpose. Its purpose here is to display the scope and detail of the application of the concept of homology as it appears serially in the plant, how homology is to be interpreted in cases of regeneration, and through this, how structures that may otherwise appear as anomalous may be effectively explained. From serial homology we may proceed to general homology, a transitive relation which rests upon the notion that "things equal to the same thing are equal to one another." We will, however, use the term "equivalent" in the sense we attribute to Lindley, rather than the term "equal," which implies detailed identity. I shall employ as exemplary the homologies of the appendages of the axis of the shoot and of the flower in the flowering plants.

#### ORGANIZATION SYSTEM OF A HIGHER PLANT

Whether an organism develops from a one-celled zygote, from a single meristematic cell, or from a group of meristematic cells, there is a pattern of organization resulting from its ontogeny that reflects the plasticity of the cell in its capacity for division and differentiation. This pattern of organization has a dual aspect. It is reflected first as an increase in structural complexity brought about simply by the continued increase and

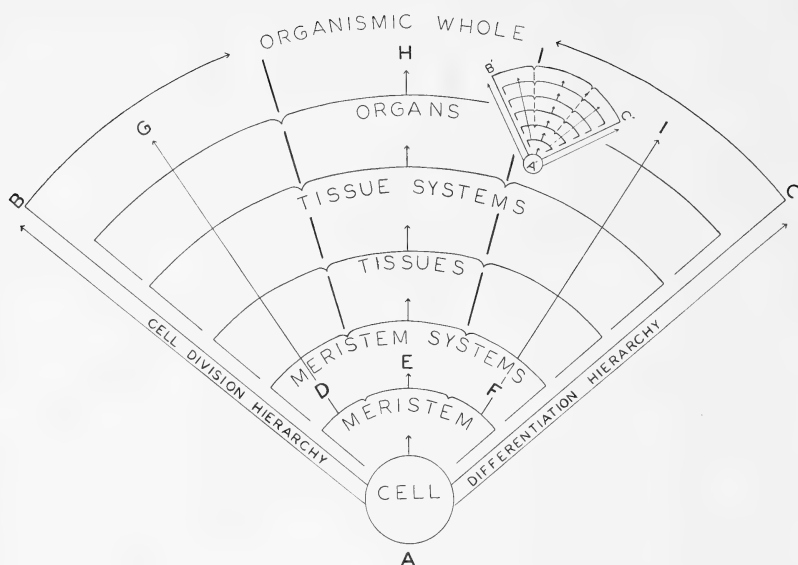


FIG. 1. Diagram of organization system resulting from increase in complexity due to cell division and cell differentiation.

A to BC represents the complexity arising purely from the multiplication of cells. The three cell lineages A to DG, A to EH, and A to FI represent differentiation through the activities within each of the three meristem systems and represent a complexity resulting from cell differentiation. Regeneration homology is indicated by A' B' C' where a new system is generated at the organ level. Interpretation is achieved by correlating A' with A, B' with B, and C' with C.

disposition of large numbers of cells, as A to BC (fig. 1), especially where the pattern results from different planes of cell division. The pattern of organization is reflected secondly as an orderly increase in complexity resulting from the differentiation of the meristem DEF and channelling the diversity into lineages of differing tissues, tissue systems, and organs ordered in accordance with their respective meristem origins, as A to DG, A to EH, and A to FI. Let us suppose that these represent the lineages originating in the three meristem systems from promeristem through protoderm, procambial strands, and ground meristem, and the cell and tissue lineages of each meristem system to its structural destiny. By superimposing the idea of increased structural complexity through cell division on different planes over that of the results of meristematic differentiation, as shown in the system chart (fig. 1), we obtain the impression of an organization system that may be of great utility in the interpretation of comparable structures on any given plant, as well as a basis for determining what on any given plant is comparable; through such serial comparison we may determine what structures on different plants are comparable. We may interpret the design as constituting a hierarchy of different levels of



organization in which each of the lower levels participates within the limits of its meristematic origin in the structural organization of each successively higher level, and at length each is an integral part of the organismic whole. Analytically this presents a design in order approachable through mathematical induction.

Aside from the cell division hierarchy and the resulting segregation mentioned above, it is also possible to trace in these same patterns hierarchies of structural specialization and of associated functional specialization. And since each phylogenetic step of structural advance was accomplished as a precise step in the ontogeny of an individual through the activity of mutagenic agencies or other cytological phenomena by which an individual deviated from its predecessors to the extent of this step, the hierarchy of organization also reflects, to a limited extent, through logical implication, the basis for a phylogenetic explanation as it relates to structural pattern. The reasoning here is clear, but because of the nature of the facts it may be clearer than the evidence. The reasoning is as follows. There is no step in phylogeny that structurally is not first evident as a step in the ontogeny of an individual regardless of its cause. So far as the empirical phenomena upon which these rest are concerned, and especially as phylogeny relates to any particular phylogenetic step, ontogeny and phylogeny are one. It is possible to abstract successive steps in phylogeny out of their context of successive ontogenies. We may then speak of a unitary phylogenetic sequence. Through the many changes that have involved the structural differentiation of plants, however, it is no longer possible to separate these as discrete historical steps in either phylogeny or ontogeny. Because of this, the ideally sound biogenetic law of Haeckel (1876) that ontogeny recapitulates phylogeny is difficult of application except in very general terms. The common properties of equivalent structures must be assumed to represent their common ancestral connections from which they deviate in their separate ontogenies and phylogenies. It would seem, therefore, that the concept of morphological equivalence rests, to this extent, on the biogenetic law. In our organization diagram, therefore, as they relate to an individual, the older phylogenetic facts are probably to be found lower in the system than are the younger. (In this predecessor-successor relation of morphological facts based upon levels of identity, we see the basis for the connected system necessary for the logic of homology.) To my thesis, the operation of the biogenetic law is most clear when a preceding structure serves as a structural foundation for a phylogenetically following structure and must be resynthesized in each ontogeny in order that the following structure may be synthesized. This may be the full scope of the meaningfulness of the biogenetic law in plants.

#### THE CELL AND ITS ROLE IN ONTOGENY

Since each individual begins as a single cell and each step in the complexity and differentiation of the whole results from cell division into like or different kinds of cells, it will be apparent that all known operational

dynamics in the structural ontogeny of the individual are on the level of dividing cells, plus any subsequent modifications of any individual cell. Dividing cells occur at nearly all structural levels of the hierarchy, and such meristematic cells, through the subsequent development of descendant cell lineages, may either carry the main organization system toward its completion or may initiate a cell lineage capable of developing a new structure that may be an ontogenetic departure from the structure in which the original cell arose. Thus at the junction of the petiole and the blade of the leaf of *Tolmiea menziesii* and in the crenations on the leaf margin of various species of *Bryophyllum*, buds develop that generate new plants as complete as those which develop from seed. Organographically these initiating meristems occur at a high level in the organization system. However, in the inception of this activity we must think of the meristems as returning to a lower level in the system and thus as regenerating a new system. It is a very important fact that neither the resulting system nor the structure produced in any way distorts the interpretation of the organ on which these initiating meristems arose. In the cases here mentioned the organs bearing the new "system" are still and always will be leaves.

How and where new anatomical lineages may develop and to what extent they develop will depend upon the "special and local predisposing causes of ontogeny." These predisposing causes may result in the production of such structures as a sporangium on a sporophyll, the extension of a structure by toral growth, the production of some teratological structure, the development of a tissue, or the extension of a vascular system. If such a structure is defined in terms of its inherent properties, it is primarily significant for what it is. Only if it is defined in terms of some positional relation is it ever significant for where it is. In some cases it may be significant to the defining type of the structure that bears it, as for instance, a megasporangium on a sporophyll is significant to this sporophyll being also a carpel; but neither what the sporangium is, nor where it is, is in any way significant to the interpretation of the carpel as being also an appendage.

Such ontogenetic and phylogenetic facts are useful in the explanations of likenesses and differences by which we classify, but they neither serve to describe nor define the classes of like structures. As we contemplate these matters we are first concerned with the identity of the structure, then with its connected relations in a classified system of structures. We discover in the properties of our material the order and connectedness that relates the classes of structures. We then explain it with our notions of ontogeny and phylogeny. Our first task is to discover and describe and thus determine what are homologous structures. We move then to explanation.

It would seem important, therefore, that if we are to seek to explain such structures and their relations, we must direct our attention first to the organization level of dividing and differentiating cells regardless of the higher organization level of which these cells may have been a part.

The primary fact is the capacity of a meristematic cell. The anatomical environment of this meristematic cell may influence the nature of what develops from it, but we must realize that when this development is complete the resulting structure may be categorically independent of the structure that originally produced the cell. What is important is the nature and identity of this resulting structure.

Through the vagaries of meristematic initiation, such structures may develop anywhere in the organization system. Where the predisposing causes of their synthesis become organized in the gene pattern, they are to be regarded as normally a part of the ontogeny of the plant and may be represented by any tissue, tissue system, or organ, or by modifications or by parts of these. In effect, in their ontogenetic elaborations they constitute organization systems of their own and can be abstractly superimposed upon the general organization system and correlated in a one to one manner with comparable structures as they may occur anywhere on the plant (fig. 1, A', B', C'). Thus parenchyma is parenchyma, anywhere on the plant, irrespective of the structure that gives rise to its initiating cell or cells. We may think of it as being related solely to the predisposing causes of parenchyma, whatever that combination of conditions and events may be. Likewise any other structure as it may occur normally or abnormally is to be regarded primarily in terms of what it is rather than the nature of its meristematic origin. What is important in each of these cases is, 'What is the structure that results from such activity?' and not, 'From where did it arise?'

#### THE CONCEPT OF HOMOLOGY

As mentioned above, the concept of homology had its origin among the ancient geometricians and was applied to biology by the anatomical philosophers at the beginning of the last century. In biology it found its first linguistic form in the doctrine of metamorphosis of Wulff and Goethe. Thus homology is not solely a biological notion. It is to Owen (1848) that we turn for most of the current notions of homology as applied in biology. Owen thought of homology as a serial system, although he expressed himself in a manner that introduced some confusion between his serial system and his example, namely the serial segmentation of animals to which he applied the notion. Homologies outside of a given serial system could be drawn wherever the necessary comparisons could be made and relations established. These relations served to connect the serial systems of diverse organisms. This Owen spoke of as establishing general homology. In view of current controversy it appears that some clarification of these notions is in order.

Homology as employed in biology is an adaptation of the notions of set theory, relations theory, and the theory of types, together aimed at establishing the formal relations between the structures of organisms (Woodger, 1937). The relations that we in biology speak of as "homology" differ from ordinary relations because the field of the relations is the

organism, which comprises a dynamic system. The relations thus imply the operations of the dynamic system that have brought them about. So compelling is this implication that to many it has become an integral part of the concept, with the dire consequences that the formality of the relations is often confused by having some anticipated notion of the implication built into it. However, the actual homology rests solely upon the formal relations in the serial system, and these should be established independently of any implication to be derived from them or to be anticipated in their behalf and independently of any explanation that may be forthcoming from our understanding or our misunderstanding.

Serial homology actually is the serial system of class relations in ascending order into which any given structure may be classified. For example, a petal of a flower belongs to the following series of classes:—petal, corolla, perianth, flower part, appendage. Each class level represents an increase in the scope of structures that are included as homologous organs. Each class expresses the homologous relation of its included terms. Thus a leaf and a petal bear the homologous relation "appendage" to one another. Each class at each level comprises a logical type.

One may insert classes or subclasses into this system as occasion may demand so long as they are inserted in a proper serial order determined by the scope of the relations that are expressed. The number of properties and the nature of the properties upon which the class is based is not important. Its position in the series is. This is because each such class stems from the logical conjunction of subclasses, and hence it represents the logical connection of the subclasses in series with the class. We thus have in the system the basis for establishing order and connectedness among the morphological properties of organisms. Through their connectedness their morphological equivalence is implied.

As one approaches the system analytically, it will be found that the basis of the implication accrues by mathematical induction, each subclass at each level adding its increment to the logical type of its predecessor to establish its own logical type. And as each new logical type is thus established, the scope of the relations expressed is thereby narrowed. The compelling feature of the implication is enhanced by the orderliness of these accruing foundations of relations and the realization that they are founded in ontogeny. Also, as they relate to the interpretations of phylogeny they give some semblance of meaning to the biogenetic law in that the properties of each predecessor class must be synthesized in ontogeny as the foundation for the synthesis of the properties of successor classes. This is solely logical implication and not logical proof. The scope of the relations of the more inclusive classes, however, is significant, since it serves to give a sequence of order to the properties.

Because of the complex nature of higher plants, the serial system must be thought of in terms of various structural levels of homology rather than in terms of a single organographic series culminating in the individual as the class that includes all. The organographic series provides a very

incomplete concept of serial homology. It should be clear that homologies are possible on different levels of organization of ontogeny. The cytologist employs the concept at the level of cells and cell contents. Here homologies of very broad scope are possible. The basis of homology rests in the identity of the structure, and it implies origin from a pre-existing similar structure. At a higher level in the system the anatomist employs the concept of homology for tissues and tissue systems. Here like or equivalent cells are organized into tissues arising from a common or equivalent meristem as they become a part of a higher organizational tissue system. In such cases the homology often becomes restricted within the scope of the ontogenetic lineage cut off in the differentiation of the promeristem into protoderm, procambium strands, and ground meristem.

A third level of homology may be spoken of as the organographic level involving identity and positional relations of organs and appendages. Here we are concerned with cells, tissues, and tissue systems constituting organs and appendages as these arise similarly from like meristems and are arranged upon a common plan.

As we ascend the levels of structural complexity, the scope of possible homologies is reduced and becomes more localized as to areas of the plant and involves fewer serial structures. Likewise, in general homology, the higher the organizational level the fewer are the homologies that can be broadly drawn. Thus, on the organographic level one is less able to draw broad homologies than one is on the level of tissues and cells. For instance, carpels are confined to the angiosperms, tracheids are present in several classes of plants, while cells are characteristic of all plants.

Because of the capacity of dividing cells to generate structures morphologically unrelated to the organ that bears them, one must recognize this state of affairs in his concept of homology. It calls for an assessment of the situation in terms of what structures result and how they may be correlated with the organization system as a whole. The homologies of such structures become evident through their identity and their assignment to the proper level in the serial system of the whole. For such homologies I shall use the term "regeneration homology."

Any deviation that is evident in a practical application of this system must seek its explanations in regeneration homology. This will be particularly evident when a structure attains properties assignable to a structure other than that on which it occurs. It will also be evident when a tissue occurs in the confines of a meristem system in which such tissues do not ordinarily arise.

#### THE NEED FOR CLEAR DEFINITIONS

In the practical application of homology to the problems for which the logical system is devised, it becomes imperative that such structures and abstractions employed be clearly as well as inclusively and exclusively defined. The chief problems in establishing homology are precisely traceable to these difficulties of definition or to semantic problems in not under-

standing the level of abstraction and the resulting error as to what criteria are involved. Whereas a sporangium may be significant to the concept "carpel," it is not significant to the concept "appendage" and has nothing to do with the inclusion of carpels as appendages. There may be many other features of carpels that may be significant to the concept of carpel or significant to the carpel of some particular kind of plant, but they play absolutely no role in the abstractions of the category "appendage" which are based upon the common characters of kinds of appendages. We are not concerned with the characters of carpels whereby they may be unlike other appendages. We are only concerned whether or not they possess the characters that are diagnostic of the abstract concept "appendage." To the extent that these characters are present, we classify the carpel as an appendage and to this extent it fulfills the classical theory as amended by Lindley. To this extent also, the assignment of the carpel to the concept "appendage" constitutes another relation step in our logical system. We must be aware, however, that logic is not self-validating, and in this case it is no more valid than is the significance of the criteria of morphological equivalence that we have accepted. The logical system is only a method of handling the facts that we accept as valid. We cannot hold the system responsible for the validity of these facts. Our logic cannot correct our mistakes, although sometimes it may assist in pointing them out.

When we find carpels that display characters that confuse us as to what structural category in which to include them, it seems to me necessary to investigate whether or not we are dealing with a simple situation or with a phenomenon that may be better handled through the logic of regeneration homology. Perhaps the occurrence of sporangia on sporophylls is such a case. Some seem to think that a sporangium is normally terminal on a cauline structure. Should this be true the problem of sporangia on appendages fits naturally into the logical system of regeneration homology. We would presume that through the predisposing causes of ontogeny a meristematic event takes place that generates a sporangium on an appendage, and these facts make of the appendage a sporophyll. When provision for the synthesis of the predisposing causes becomes organized in the gene system, the production of sporangia on appendages is normal. Such an event in no way destroys the homologies of the sporophyll as an appendage. It is in every way comparable to the occurrence of buds on the margin of the leaf of *Bryophyllum*.

I deliberately employed the sporangium in this example because it was easy to discuss and seemed to fit in well as an example. There are other stem-like tissues reported in carpels that have raised questions of their reference to appendages. The explanations of these should be sought upon an anatomical level of homology and evidence sought as to what structures are represented and what has been their ontogenetic history. Next the problem is to find the extent of their organization and what their resulting homologies may be.

The fact that we seek identity in the old does not mean that new struc-

tures might not appear and that new structures are not possible in the gynoeceum. It does mean that before we can assign them as being new structures, we must have some criteria other than our confusion in the interpretation of the old, upon which to base our decision. A new structure is one which does not possess the diagnostic criteria that would permit it to be classified in any existing category of structures at the same organization level.

Much of this confusion stems from lack of clarity as to what constitutes any particular organ or structure. For example, much of the problem of the inferior ovary stems from the fact that we do not have an adequate definition of a receptacle drawn from characters that are diagnostic of a receptacle. The result has been that we seek evidence of receptacles in criteria that are not diagnostic of such a structure, as, for example, the employment by Smith (1943) of recurrent bundles in the structures surrounding the ovary in Santalaceae as evidence that this structure is a receptacle. If the structure surrounding the inferior ovary and traversed by the recurrent bundles in the Santalaceae is a receptacle, it must be so on some other evidence, for recurrent bundles are not diagnostic of receptacles, nor are branched or unbranched bundles so diagnostic. In seeking diagnostic criteria for the receptacle, about all that I can find common to the several hundred kinds of flowers I have examined is that the receptacle of all of them bears flower parts and is at least operationally terminal on an axis. I have seen no evidence whatsoever in the vascular system that provides for a universally applicable set of criteria by which one might recognize a receptacle as different from any other structure related to stems. We must bear in mind that the plant does not define "receptacle." We as humans define it, and we define it for our own devices.

#### ON THE ROLE OF THE TELOME

If the telome-mesome complex is significant in the interpretations of morphology, it cannot be employed in any problem of diagnostic comparison that employs the logic of homology above the level of meristem differentiation in the organization system. This is because the telome, like the cell, is a ubiquitous structure. It is presumed to be a characteristic of everything and therefore cannot be diagnostic of anything. The logic of homology follows strictly the pattern of diagnostic comparison. To be significant, an attribute must be diagnostic. The cell is significant to homology only on a cytological level where cells are compared with cells. If the telome is significant to homology, it can be significant only on levels where telomes are significant to the diagnosis of the structure. It may be possible to make such diagnoses on the basis of kinds of telome systems if these are valid structures.

#### CONCLUSION

This reorganization of our logical system I believe will give us at least a sound working hypothesis for the flower which we can use in developing

our concepts of phylogenetic taxonomy. The concept of homology, because of its ontogenetic implications and because phylogeny also has ontogenetic implications, provides us with the necessary basis for handling the problems of likenesses and differences as they involve comparable structures. There is no problem of phylogenetic divergence, as it is subject to investigation in taxonomy, that is not pursued from the point of view of the logic of the concept of homology as it relates to the properties of organisms.

When we turn from the plant to contemplate what we have seen and to interpret its significance, we must inevitably rely either upon the intuitive judgments of what appear to be immediately self-evident facts, or we automatically resort to a logical system based upon reasoning. The one is the intellectual foundation of sight recognition, the other the intellectual foundation of identification. Both have an important place in interpretive science. Neither is self-validating and therefore either may lead to erroneous judgments. The security of the one rests in the validity of the immediate self-evidence. The security of the other, as it relates to our problem, rests first in the validity of the logical system and then in the validity of the diagnostic criteria.

It therefore becomes important that we develop an adequate logical system such as we strive for in perfecting the system of homology. It is also important that we seriously re-examine the validity of the diagnostic criteria of the structures and the abstractions that we employ as significant to our interpretations. Upon this will rest the validity of their self-evidence, so important to our intellectual manipulations.

We must not assume that simply because we may have more detailed and complete facts, as important as this is, that we can avoid operating within the framework of intuitive judgment and logical systems in our interpretation. If we had all of the facts of structure and ontogeny, we would only shift in our intellectual contemplation of them from a preponderant leaning upon logical systems to a heavier reliance upon intuitive judgment. This is because sight recognition would play a greater role. The validity of our judgments will still rest upon individual human capacities for discrimination as to significance. We still will be plagued by the curse of him who, without understanding them, employs the faulty judgments made by himself or others. The plant is responsible for what is there. What the plant and its structures mean to us is our responsibility, and it is not solely a responsibility of discovery, important as this is, because discoveries must be interpreted to be understood.

Department of Botany,  
University of California, Berkeley.



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## MITOTIC CHROMOSOME STUDIES IN THE GENUS ASTRAGALUS<sup>1</sup>

S. CONRADE HEAD

The genus *Astragalus* L., tribe Galegeae of the Leguminosae, consists of about 1,500 species occurring in northern Africa, Europe, northern and central Asia, and in the western hemisphere. Some sixty genera have been proposed as segregates from it, and several taxonomic revisions of the genus or parts of it for North America, based on morphological characters, have been presented (Jones, 1923; Rydberg, 1929; Barneby, 1945, 1947, 1949, 1956). Of these, the more conservative treatments of Jones and Barneby have been found more practical for the purposes of this study.

Very little, however, is known about the cytology of this genus. According to Senn (1938), "Only two per cent of the species of the huge genus *Astragalus* have been studied. These species are based on an 8 series with

<sup>1</sup> This paper represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Botany at the State College of Washington, Pullman. 1955.

two exceptions in which  $n=14$ . There are 16 diploids, 1 tetraploid, 2 hexaploids, and 1 octaploid. Considering that the species studied come from widely separated regions scattered over Europe and Asia, this is a remarkable consistency of chromosome number." According to Tischler (1938), the findings of ten workers for forty-four Old World species and four New World species were:  $2n=16$ , thirty-three species;  $2n=32$ , three species;  $2n=48$ , four species;  $2n=64$ , five species;  $2n=28$ , 36 and 96, one species each. Vilkomerson (1943) made a survey of twenty-six species from western United States and found that for eleven  $2n=24$ , for thirteen  $2n=22$ , whereas the other two had  $2n$  numbers of 16 and 44 respectively. James (1951) gave chromosome counts for three species, one each of  $2n=22$ , 24 and 26. These several surveys account for approximately one hundred species of *Astragalus*. Certainly the consistent chromosome number stressed by Senn no longer holds. It was with the thought of adding to the chromosomal information for this genus that the present investigation was undertaken.

The author wishes to express his appreciation to Dr. Adolph Hecht, who served as advisor during the course of the research and who with Dr. Marion Ownbey kindly offered many suggestions during the preparation of the manuscript. Mr. Robert C. Barneby provided several of the collections reported here and checked many of the determinations. Mr. Ralph D. Amen offered many valuable suggestions concerning cytological methods.

#### METHODS

The *Astragalus* collections studied are listed by species in Table 1. The source of the collection, the chromosome number, and the figure number (for those collections illustrated) are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The plants were grown in the greenhouse and later transplanted to an experimental garden at Pullman, Washington. Seeds had to be scarified either by filing or by use of concentrated sulfuric acid, with treatment in the acid from forty-five minutes to one hour being most satisfactory. The scarified seeds were placed on wet filter papers in Petri dishes until the primary root had reached a length of about fifteen mm.; the root was then removed and placed in Belling's "metaphase" modification of Navashin's solution. Root tips were also obtained from pot-bound plants. Some plants were transplanted from their natural habitat to the greenhouse and later to the garden. Since most persons preparing herbarium specimens rarely collect mature fruits, herbarium sheets did not prove to be a profitable source of seed. A few seeds were obtained from herbarium sheets, however, and those as old as nine years germinated without great difficulty provided they were mature when collected.

Paraffin sections cut at twelve microns as recommended by Senn were prepared and stained by the crystal violet-iodine method. These preparations were not as satisfactory as those obtained by a method worked out

by Amen (unpublished).<sup>2</sup> This method provides excellent permanent slides with the cells separated from each other. One has little difficulty in viewing separated cells under the microscope, and the observer is certain that the cells are uncut. Amen plans to publish his method in detail. My modification of his procedure is as follows:

Fix cut root tips in Belling's "metaphase" modification of Navashin's solution preferably for at least two days; remove, rinse several minutes in tap water, blot off excess water; place on slide in one drop of Haupt's adhesive; cut apical 2 mm. into several pieces and squash, using flat side of scalpel; air dry slide about 15 minutes; stain in 1 per cent methyl violet for 10 minutes, wipe off excess stain and nearly air dry; wash momentarily and again nearly air dry; place in solution of 8 grams of picric acid powder dissolved in 1 liter of 95 per cent alcohol for about 20 seconds; blot excess 1 to 2 seconds, place in absolute alcohol about 20 seconds; clear in 50 parts absolute alcohol, 25 parts xylene, and 25 parts clove oil for 3-7 minutes; pass through 2 changes of xylene; mount in piccolyte.

Slides were examined and camera lucida drawings were made of the metaphase plates using a Zeiss microscope with an apochromatic oil-immersion lens of N. A. 1.30 and an initial magnification of 2,250 times. The figure were drawn at approximately 4,350 times and reduced to 1,450 times in reproduction.

TABLE 1. CHROMOSOME NUMBERS OF ASTRAGALUS COLLECTIONS STUDIED

SPECIES	CHROMOSOME NUMBER (2n)	FIGURE NUMBER	SOURCE
SECTION HOMALOB <sup>3</sup>			
<i>A. stenophyllus</i> T. & G.	24	1	Oregon, Morrow County: 12.9 miles southwest of Heppner, <i>Head 598</i> .
	24	2	Oregon, Baker County: 12.5 miles southeast of Baker on the Ebell Creek Road, <i>Head 609</i> .
	24	3	Oregon, Wheeler County: 16 miles south of Condon, <i>Head 600</i> .
SECTION INFLATI			
<i>A. lentiginosus</i> Dougl. ex Hook. var. <i>lentiginosus</i>	22	4	Oregon, Baker County: 1 mile east of Quartz, <i>Head 607</i> .
<i>A. cusickii</i> A. Gray	22	5	Washington, Asotin County: near the Grande Ronde River bridge, <i>Head 569</i> .
	22, 44* <sup>4</sup>	36	Oregon, Baker County: 13 miles west of Richland, <i>Head 611</i> .

<sup>2</sup> Amen, Ralph D., former graduate student, State College of Washington. Present address: 2426 South University, Denver, Colorado.

<sup>3</sup> Sections are those listed by Jones (1923) although this arrangement is not always satisfactory.

<sup>4</sup> Diploid and tetraploid cells occur in the same root tip of many Leguminosae. See discussion on polysomaty. Such counts are indicated by an asterisk.

SPECIES	CHROMOSOME NUMBER (2n)	FIGURE NUMBER	SOURCE
<i>A. beckwithii</i> T. & G. var. <i>weiserensis</i> M. E. Jones	22	6	Idaho, Owyhee County: 10 miles north of Silver City, on road to Murphy, <i>Christ</i> 19537.
<i>A. allochrous</i> A. Gray	22	7	New Mexico, Grant County: San Lorenzo, <i>Barneby</i> 11172.
SECTION COLLINI			
<i>A. collinus</i> (Dougl. ex Hook.) G. Don var. <i>collinus</i>	24, 48*	8, 37	Washington, Asotin County: 5.5 miles northeast of Anatone, <i>Head</i> 585.
	24	9	Washington, Asotin County: 6.3 miles northeast of Anatone, <i>Head</i> 588.
var. <i>laurentii</i> (Rydb.) Barneby	24	10	Oregon, Morrow County: 18.6 miles east of Heppner, <i>Head</i> 596.
SECTION HAMOSI			
<i>A. andersonii</i> A. Gray	24	11	Nevada, Washoe County: 6 miles northwest of Univ. of Nevada Campus, Reno, <i>Ownbey</i> 2925.
<i>A. arthurii</i> M. E. Jones	24	12	Washington, Asotin County: 3.4 miles northeast of Anatone, <i>Head</i> 587.
<i>A. congdonii</i> S. Wats.	26, 52*	13, 39	California, Fresno County: Piedra, <i>Barneby</i> 11417.
SECTION PODO-SCLEROCARPI			
<i>A. sclerocarpus</i> A. Gray	22	14	Washington, Benton County: 2 miles west of Enterprise (West Richland), <i>Head</i> 525.
<i>A. pachypus</i> Greene	22	15	California, Kern County: Caliente, <i>Barneby</i> 11370.
SECTION REVENTI-ARRECTI			
<i>A. arrectus</i> A. Gray	24	16	Washington, Whitman County: Prairie Strip, Botany Dept. State College of Washington, Pullman, <i>Head</i> 584.
<i>A. sheldonii</i> (Rydb.) Barneby	24	17	Washington, Asotin County: 3.4 miles northeast of Anatone, <i>Head</i> 586.
<i>A. riparius</i> Barneby	24	18	Washington, Whitman County: 3.3 miles northeast of Wawawai, <i>Head</i> 562.

SPECIES	CHROMOSOME NUMBER (2n)	FIGURE NUMBER	SOURCE
	24	19	Washington, Whitman County: 1.1 miles east of Wawawai, <i>Head</i> 563.
<i>A. conjunctus</i> S. Wats.	24	20	Oregon, Wheeler County: 16 miles south of Condon, <i>Head</i> 599.
<i>A. eremeticus</i> Sheldon var. <i>malheurensis</i> (Heller) Barneby	24	21	Idaho, Washington County: just north of Weiser, <i>Ownbey</i> 2761.
SECTION ULIGINOSI			
<i>A. canadensis</i> L. var. <i>mortonii</i> (Nutt.) S. Wats.	16	22	Washington, Whitman County: north slope of Kamiak Butte, <i>Head</i> 613.
SECTION CHAETODONTES			
<i>A. spaldingii</i> A. Gray	24	23	Washington, Whitman County: ½ mile east of Lacrosse, <i>Head</i> 582.
SECTION ARGOPHYLLI			
<i>A. inflexus</i> Dougl. ex Hook.	22	24	Washington, Whitman County: 1 mile northeast of Wawawai, <i>Head</i> 499.
<i>A. purshii</i> Dougl. ex Hook. var. <i>glareosus</i> (Dougl. ex Hook.) Barneby	22, 44*	25, 38	Oregon, Baker County: 1 mile east of Quartz, <i>Head</i> 547.
	22	26	Oregon, Morrow County: 18.6 miles east of Heppner, <i>Head</i> 595.
	22	27	Oregon, Grant County: 2.5 miles north of Mt. Vernon, <i>Head</i> 603.
	22	28	Oregon, Grant County: 2.4 miles north of Mt. Vernon, <i>Head</i> 604.
var. <i>purshii</i>	22	29	Washington, Whitman County: top of Steptoe Butte, <i>Head</i> 580.
<i>A. chamaeleuce</i> A. Gray	22	30	Colorado, Mesa County: 3 miles south of Fruita, <i>Weber</i> 3782.

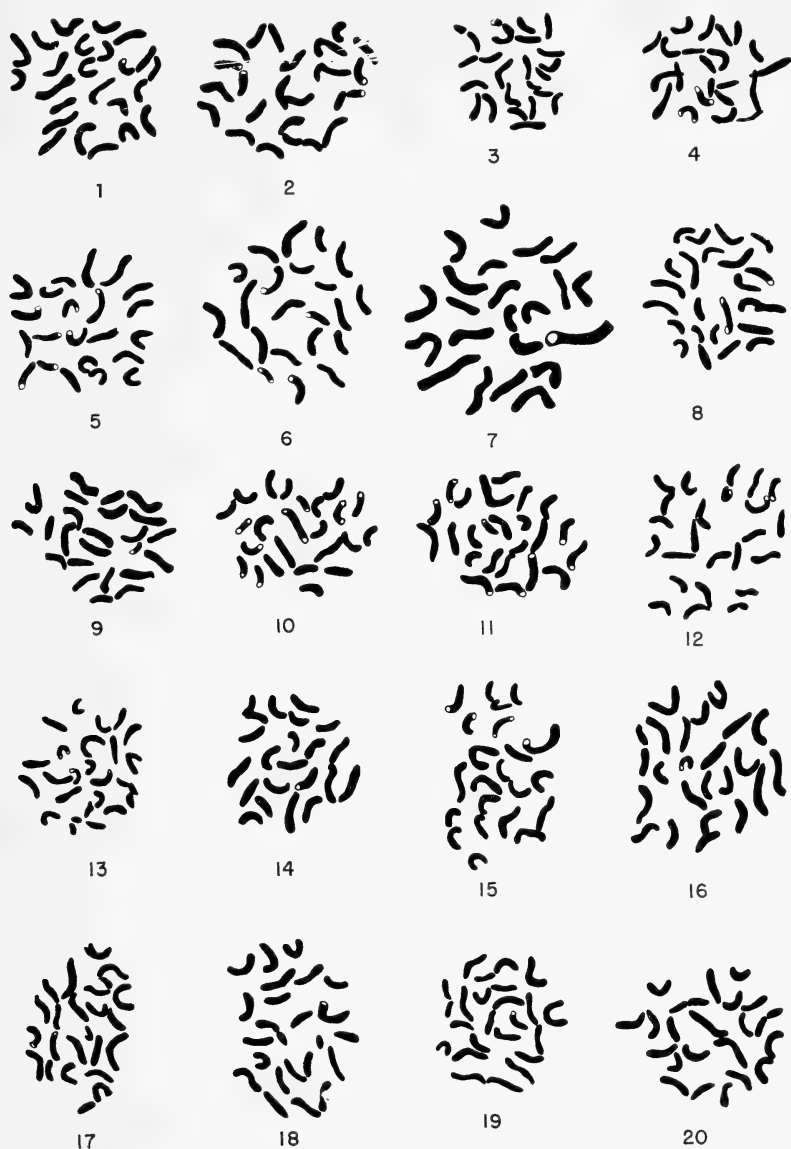
SPECIES	CHROMOSOME NUMBER (2n)	FIGURE NUMBER	SOURCE
<i>A. cibarius</i> Sheldon	22	31	Idaho, Bannock County: 12 miles south of Portneuf, <i>Christ</i> 19933.
SECTION MALACI			
<i>A. succumbens</i> Dougl. ex Hook.	24	32	Washington, Walla Walla County: 7.4 miles east of Wallula, <i>Head</i> 539.
SECTION MOLLISSIMI			
<i>A. mollissimus</i> Torr. var. <i>earlei</i> (Rydb.) Tidest.	24	33	Texas, Jeff Davis County: southeast of Fort Davis, <i>Barneby</i> 11129.
SECTION SARCOCARPI			
<i>A. gypsodes</i> Barneby	24	35	New Mexico, Eddy County: southwest of Whites City, <i>Barneby</i> 11138.
SECTION UNDETERMINED			
<i>A. diaphanus</i> Dougl. ex Hook.	28	34	Oregon, Wheeler County: 2 miles east of Service Creek, <i>Hitchcock</i> 19235.

### DISCUSSION

As the table indicates, chromosome numbers of  $2n=16$ , 22, 24, 26, and 28 were found in the plants studied. The sections *Inflat*i, *Collini*, *Podo-sclerocarpi*, *Reventi-arrecti* and *Argophylli* showed constant chromosome numbers. The section *Hamosi* had two different chromosome numbers represented; *A. andersonii* and *A. arthurii* both had  $2n=24$ , and *A. congdonii*,  $2n=26$ . A like situation was reported by Vilkomerson (1943) for the section *Galegiformes*. Even prior to her publication, the need for a taxonomic revision considering physiological evidence was suggested by Trelease (1942). Vilkomerson also reported a chromosome number of  $2n=22$  for *A. crassica*rpus Nutt.; *A. gypsodes* is recorded above as having  $2n=24$ . Barneby (1956) groups these two species together in the same section. James (1951) found three different chromosome numbers represented by three species in the section *Didymocarpi*. Thus we see it is possible for a section to have species with different chromosome numbers. Yet, as cytological information accumulates for the genus, more sections are found to have a constant chromosome number. Much more study is needed in the section *Hamosi* and, as Trelease mentioned, in the *Galegiformes*.

Certain species of *Astragalus* can be readily identified by their characteristically shaped chromosomes. Among these are *A. succumbens* with a pair of large "question mark" chromosomes and *A. mollissimus* var. *earlei*

with its eight pairs of "C" chromosomes. The sections *Reventi-arrecti* and *Argophylli* may also be recognized by chromosome similarities of the included species.



FIGS. 1-20. Chromosomes of *Astragalus*. 1-3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8-9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18-19, *A. riparius*; 20, *A. conjunctus*. Camera lucida drawings,  $\times 1450$ .

SECTION HOMALOBII (figs. 1–3, idiograms 1–3).—Geographical distribution of *A. stenophyllus* appears to have little correlation with chromosome morphology in this species. Figures 2 and 3 are from plants which grew about two hundred miles apart, yet the chromosomes appear more alike than those of figures 1 and 3 which are from plants separated by only a few miles.

SECTION INFLATI (figs. 4–7, 37; idiograms 4–7).—In all of the *Inflati* so far studied the  $2n$  number is 22, provided *A. diaphanus* is not referred here. However, the section as a whole cannot be characterized or identified on the basis of chromosome similarity, for the positions of the centromeres are not as consistent as in those groups already mentioned. Both *A. allochrous* and *A. cusickii* have four pairs of chromosomes with nearly median centromeres which take a characteristic “C” shape. *A. beckwithii* var. *weiserensis* has but one pair of these chromosomes. *Astragalus allochrous* (fig. 7) has the largest chromosomes of any found in this study.

SECTION COLLINI (figs. 8–10, idiograms 8–10).—In contrast to the low correlation of chromosome morphology with geographical distribution in *A. stenophyllus* of section *Homalobi*, here there is much similarity in chromosome morphology from plants separated by even greater distances.

SECTION HAMOSI (figs. 11–13, idiograms 11–13).—The two species with the 24 chromosomes, *A. arthurii* and *A. andersonii*, have little in common with the 26 chromosome species *A. congdonii*. The latter (fig. 13) has five pairs of “C”-shaped chromosomes, while the former two species have only two pairs. *Astragalus arthurii* is unique in that one chromosome (the last in idiogram 12) shows a prominent constriction at about the middle, which might be the centromere region. Chromosomal data beyond that now available should be obtained before a revision of the *Hamosi* is attempted.

SECTION PODO-SCLEROCARPI (figs. 14–15, idiograms 14–15).—Vilkomerson studied nine species belonging here, including *A. sclerocarpus*, and found the same chromosome number ( $2n=22$ ) in all. *A. pachypus* is the only new report for a species of this section. Unlike *A. sclerocarpus* (idiogram 14), *A. pachypus* (idiogram 15) has several pairs of “C”-shaped chromosomes.

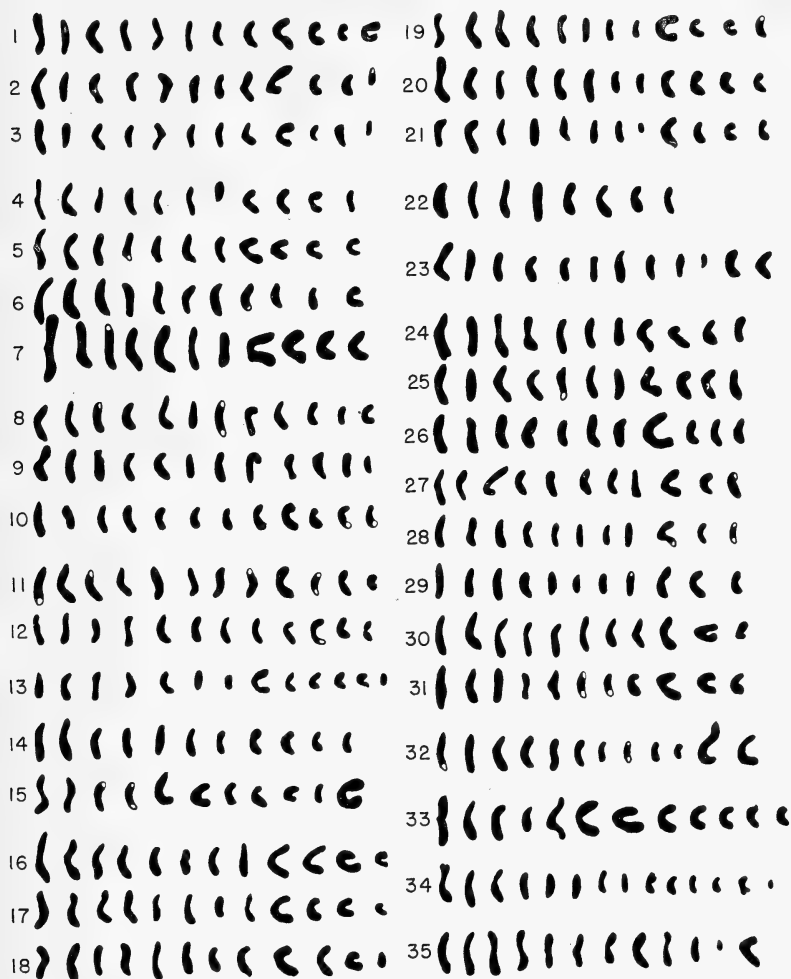
SECTION REVENTI-ARRECTI (figs. 16–21, idiograms 16–21).—Members of this section have very similar chromosomes. Each of the five species studied has four pairs of “C”-shaped chromosomes. Although these chromosomes vary somewhat in length they are otherwise very similar. *Astragalus eremiticus* var. *malheurensis* (idiogram 21) differs somewhat from the others by having a pair of small “dot” chromosomes not found elsewhere in this section.

SECTION ULIGINOSI (fig. 22, idiogram 22).—Only one species of the *Uliginosi* has been studied, *A. canadensis* L., reported by Vilkomerson, and *A. canadensis* var. *mortonii* of this study.

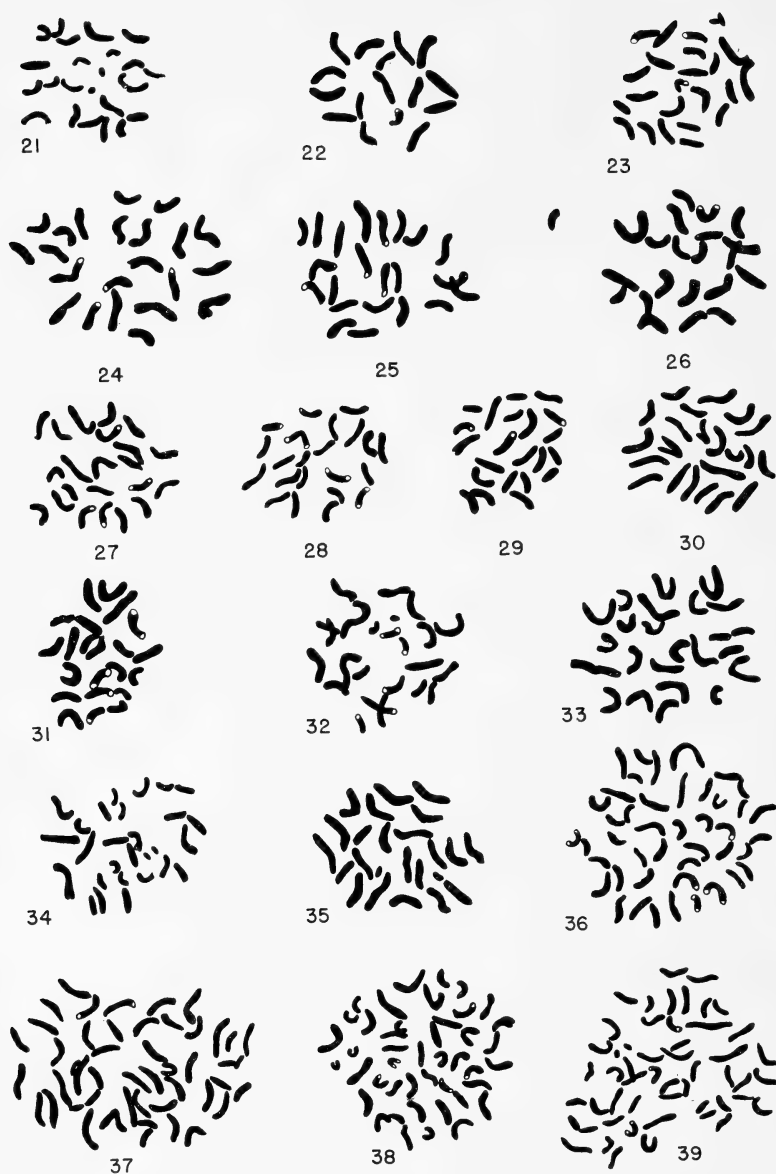
SECTION CHAETODONTES (fig. 23, idiogram 23).—*A. spaldingii* is the only member of this section thus far studied.



SECTION ARGOPHYLLI (figs. 24–31, 38; idiograms 24–31).—The *Argophylli*, as a section, show a close likeness in chromosome morphology and number. This similarity is perhaps to be expected with closely related species such as *A. inflexus* and *A. purshii*, but it would not necessarily



IDIAGRAMS 1–35. Chromosomes of *Astragalus*. 1–3, *A. stenophyllus*; 4, *A. lentiginosus* var. *lentiginosus*; 5, *A. cusickii*; 6, *A. beckwithii* var. *weiserensis*; 7, *A. allochrous*; 8–9, *A. collinus* var. *collinus*; 10, *A. collinus* var. *laurentii*; 11, *A. andersonii*; 12, *A. arthurii*; 13, *A. congdonii*; 14, *A. sclerocarpus*; 15, *A. pachypus*; 16, *A. arrectus*; 17, *A. sheldonii*; 18–19, *A. riparius*; 20, *A. conjunctus*; 21, *A. eremiticus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25–28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibaricus*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes*. Camera lucida drawings,  $\times 1450$ .



FIGS. 21-39. Chromosomes of *Astragalus*. 21, *A. eremicus* var. *malheurensis*; 22, *A. canadensis* var. *mortonii*; 23, *A. spaldingii*; 24, *A. inflexus*; 25-28, *A. purshii* var. *glareosus*; 29, *A. purshii* var. *purshii*; 30, *A. chamaeleuce*; 31, *A. cibarius*; 32, *A. succumbens*; 33, *A. mollissimus* var. *earlei*; 34, *A. diaphanus*; 35, *A. gypsodes*; 36, *A. cusickii*; 37, *A. collinus* var. *collinus*; 38, *A. purshii* var. *glareosus*; 39, *A. congonii*. Camera lucida drawings,  $\times 1450$ .

extend to such distant species as *A. chamaeleuce* from Colorado or to *A. cibarius* from southeastern Idaho. It would be interesting to determine if this similarity is maintained throughout this large section. *Astragalus cibarius* is excluded from the *Argophylli* by Barneby (1947), and he suggests a relationship with the *Malaci* for this species. On the basis of chromosome morphology and number, however, it seems very much like the other *Argophylli* and very little like the only representative of the *Malaci*, *A. succumbens*, thus far studied.

SECTION MALACI (fig. 32, idiogram 32).—*Astragalus succumbens* has one pair of large "C"-shaped chromosomes and a pair of "question mark"-shaped chromosomes.

SECTION MOLLISSIMI (fig. 33, idiogram 33).—*Astragalus mollissimus* var. *earlei* has eight pairs of "C"-shaped chromosomes.

SECTION SARCOCARPI (fig. 35, idiogram 35).—*Astragalus gypsodes* has 11 pairs of relatively long chromosomes and 1 pair of very short ones.

*Astragalus diaphanus* (fig. 34, idiogram 34) has not been determined as to section. This species stands alone among the North American species studied in that the  $2n$  chromosome number is 28. The chromosomes are also the smallest observed in this study. Jones (1923) listed *A. diaphanus* as a variety of *A. lentiginosus*, a member of his section *Inflati*. Barneby (1945) excluded *A. diaphanus* from his section *Diplocystium* (composed of the varieties of *A. lentiginosus*), but did not propose a new status. *A. diaphanus* should be excluded from the *Inflati* on the bases of chromosome number and fruit morphology. These reasons also support Barneby's exclusion of it from the *Diplocystium*.

POLYSOMATIC CELLS. In *Astragalus*, as in many other genera of the Leguminosae, both diploid and tetraploid cells may be found in the same root tip. Vilkomerson reported polysomaty in three species, but listed its occurrence as rare. Polysomatic cells were found by Tschechow (1930) in two of the species he studied. In one of these, *A. candidissimus*, tetraploid cells were found in forty per cent of the metaphase plates. Polysomatic cells were observed in four of the taxa of the present study: *A. cusickii*, *A. purshii* var. *glareosus*, *A. collinus* var. *collinus*, and *A. congonii* (figures 36, 37, 38 and 39). In the last three species the occurrence of such cells are rare, but *A. cusickii* had about the same percentage of tetraploid cells found by Tschechow in *A. candidissimus*.

#### SUMMARY

Mitotic chromosome studies were made of twenty-six species of *Astragalus* represented by thirty-five collections. The  $2n$  chromosome numbers of 16, 22, 24, 26 and 28 were found. The basic number of 14 is added to those previously reported for the North American species. Chromosome numbers for species of the sections *Homalobi*, *Collini*, *Hamosi*, *Reventarrecti*, *Argophylli*, *Chaetodontes*, *Malaci* and *Mollissimi* are reported for the first time. Counts for three species substantiate those previously published. Certain species and some sections of the genus can be readily rec-

ognized on the basis of chromosome morphology. *Astragalus diaphanus* should be excluded from the *Inflat*i on the basis of chromosome number and morphology.

Department of Botany,  
Oregon State College  
Corvallis, Oregon

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## INNOVATIONS IN DUDLEYA

REID MORAN

As a thesis at the University of California, I prepared a revision of *Dudleya* (Crassulaceae). This revision is not yet ready for publication and may not be ready for several years. Meanwhile, two floras including *Dudleya* are nearly completed, and there is immediate need for certain names from the thesis. Therefore, one new subspecies will be described and several new combinations proposed. Abbreviations for the names of herbaria are according to Lanjouw and Stafleu (1956).

DUDLEYA ABRAMSII Rose subsp. **murina** (Eastwood) Moran, comb. nov. *Dudleya murina* Eastwood, Proc. Calif. Acad. IV. 20: 147. 1930.

DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. **gigantea** (Rose) Moran, comb. nov. *Dudleya gigantea* Rose in Britton & Rose, Bull. N.Y. Bot. Gard. 3: 23. 1903.

DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. **marcescens** Moran, subsp. nov. A subspeciebus ceteris caudicibus tenuioribus, rosulae

foliis minoribus aestate marcescentibus, inflorescentiis simplicioribus differt (fig. 1).

Caudex 1–3 cm. long, 2–7 mm. thick, often branching; rosettes 3–6 cm. wide, of 8–12 (–15) leaves; rosette leaves green, oblanceolate, acute to subobtusate,  $1\frac{1}{2}$ –3 (–4) cm. long, 5–12 mm. wide, 1–2 mm. thick; floral stems 4–10 cm. tall, their leaves deltoid-lanceolate,  $\frac{1}{2}$ – $1\frac{1}{2}$  cm. long; inflorescence of 1–2 cincinni, each 1–3 cm. long and with 2–5 flowers; pedicels erect, 5–12 mm. long; sepals deltoid, acute,  $2\frac{1}{2}$ –4 mm. long; petals bright yellow often marked with red, 10–14 mm. long,  $2\frac{1}{2}$ – $3\frac{1}{2}$  mm. wide, connate ca.  $1\frac{1}{2}$  mm.



FIG. 1. *Dudleya cymosa* (Lemaire) Britton & Rose subsp. *marcescens* Moran, subsp. nov. (type collection)  $\times 0.6$ .

Type: Shaded rocky slope by the creek, Little Sycamore Canyon, Sierra Santa Monica, Ventura County, California (near  $34^{\circ} 05'N$ ,  $118^{\circ} 57'W$ ), at about 330 meters elevation, May 28, 1948, *Moran 3078* (UC 917950).

Specimens examined: known only from the type locality, Little Sycamore Canyon, *Moran 1890* (CU), *2072* (UC), *3078* (type: UC; isotypes DS, POM).

Illustration: Des. Pl. Life 8: 70. 1936. The plant shown in this photograph is very lax, apparently as a result of cultivation.

Uhl and Moran (1953, p. 495, under *Dudleya* sp. affin. *D. ovatifolia*) reported a gametic number of 17 chromosomes in each of two collections of *D. cymosa marcescens*. Thus, like the other subspecies of *D. cymosa*, this plant is diploid with relation to the basic number for the genus.

The subsp. *marcescens* appears to be the most distinctive of the subspecies recognized here for *D. cymosa*. It is quite different from the subsp. *cymosa*, of central California, but in some respects these two are connected by the subsp. *ovatifolia*, which also occurs locally in the Sierra

Santa Monica. The subsp. *marcescens* appears to be quite distinct from the subsp. *ovatifolia*, differing in its more slender caudex, in its narrower rosette leaves, and in the withering of its rosette leaves in summer.

The only other member of the subgenus *Dudleya* known to be completely leafless in summer is *D. parva* Rose & Davidson. That also is a small diploid plant very local in Ventura County: it occurs about 8 miles north of Little Sycamore Canyon. *Dudleya parva* is quicker to lose its leaves in summer and slower to produce new ones after the first rains. It differs from *D. cymosa marcescens* further in its narrower rosette leaves, its much shorter pedicels, and its less sharply acute petals, which are pale yellow rather than bright yellow. For description and photographs of *D. parva*, see Moran, 1948.

DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. **minor** (Rose) Moran, comb. nov. *Dudleya minor* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 19. 1903.

DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. **ovatifolia** (Britton) Moran, comb. nov. *Dudleya ovatifolia* Britton in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 20. 1903.

DUDLEYA CYMOSA (Lemaire) Britton & Rose subsp. **setchellii** (Jepson) Moran, comb. nov. *Cotyledon laxa* (Lindley) Brewer & Watson var. *setchellii* Jepson, Fl. West. Mid. Calif. 267. 1901.

**Dudleya hassei** (Rose) Moran, comb. nov. *Stylophyllum Hassei* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 35. 1903.

DUDLEYA SAXOSA (M. E. Jones) Britton & Rose subsp. **aloides** (Rose) Moran, comb. nov. *Dudleya aloides* Rose in Britton & Rose, Bull. N. Y. Bot. Gard. 3: 15. 1903.

DUDLEYA SAXOSA (M. E. Jones) Britton & Rose subsp. **collomiae** (Rose) Moran, comb. nov. *Dudleya Collomae* Rose in Morton, Des. Pl. Life 6: 68. 1934.

San Diego Natural History Museum,  
San Diego, California.

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#### NOTES AND NEWS

CLEISTOGAMY IN *MIMULUS DOUGLASII* GRAY. In 1938, J. T. Howell described a small cleistogamous-flowered *Mimulus* as *M. cleistogamus* (Leaf. West. Bot. 2: 79), but he later (op. cit. 3: 127-128. 1942) recognized it as merely a "growth phase" of *M. Douglasii*. My own observations indicate the frequent presence of cleistogamous flowers in *M. Douglasii*. Their presence seems to be related to absence of sufficient water in the soil. Normally these plants grow in thin soil over sandstone, and, in years when late winter and early spring rains come often enough, they produce large open flowers. In some situations, for example, where the soil is extremely thin on

southern exposures, this seldom happens, and year after year, only cleistogamous flowers are produced.

A colony was once seen where apparently the water supply was cut down at a critical moment, following which some of the plants produced small open flowers some of which were abnormal for *M. Douglasii* (V. F. Hesse 918, Jepson Herbarium, University of California, Berkeley). One of these small flowers was observed to resemble in shape the flowers of *M. Congdonii* Robinson. Although *M. Congdonii* grows in the same area, it apparently requires a somewhat deeper soil, and has not been observed to produce cleistogamic flowers. These observations were made in the Boulder Creek area of Santa Cruz County. —V. F. HESSE, Boulder Creek, California.

NOTES ON CALIFORNIA GRASSES. Three summer weedy annual grasses are extending their range northward in California. They occur on wet soils, periodically flooded by irrigation during the summer months. Specimens cited are at the Agronomy Herbarium, University of California, Davis.

1. *ERIOCHLOA CONTRACTA* Hitchc. (prairie cupgrass). Generally of sparse occurrence in the state. Introduced from the Great Plains originally into southern California. William H. Allison collected the grass in Merced County in 1939 and the author discovered it in northern Solano and southern Yolo counties (Crampton 3147, 3148) in the summer of 1955. Apparently well-established here and competing successfully with *Echinochloa crus-galli* and *Echinochloa colonum*.

2. *CHLORIS VIRGATA* Swartz (feather fingergrass). Occurs mostly in southern California and the San Joaquin Valley. Collection of the grass from near Davis, Yolo County (Crampton 3140), and Pentz, Butte County (Morse, Farm Advisor, Butte County), confirms its northward extension. The plant has been reported seen near Auburn, Placer County, but no voucher is available.

3. *LEPTOCHLOA FASCICULARIS* (Lam.) Gray (sprangletop). This is now a very common weedy grass preferring wet habitats ranging from loose, sandy soils of stream and river shores to heavy adobe or alkaline soils of valley plains and river bottomlands. In its early development, the grass probably behaves as an aquatic, since maturing plants are often partially immersed in water, particularly in and around rice fields. Distribution of the grass in California may be designated as follows:

Infrequent: in the Coast Ranges from San Francisco Bay south to Lower California; alkaline soils east of the Sierran Crest from Lassen County south to Inyo County. Abundant: Great Valley, Butte County south to Kern County.

*AGROSTIS TANDILENSIS* (O. Kuntze) Parodi (*A. kennedyana* Beetle). This rare annual grass, previously known in California only from San Diego County, was discovered in Solano County (Crampton 3275, 3289, 3296, 3300) during April, 1956. The general area of occurrence of this species begins about 7.5 to 8 miles south of Dixon, on the road to Rio Vista, centers around Dozier Station, and extends southward for several miles. The area habitat is one of a valley plain with low and small to large hummocks interspersed with hog wallows or vernal pools that are largely alkaline and support tufts of the rhizomatous *Distichlis* along with *Eryngium*, *Deschampsia danthonioides*, *Baeria*, and *Pogogyne*. The hummocks support largely the Mediterranean annual grasses *Bromus mollis*, *Bromus rigidus*, *Festuca bromoides* and close allies, *Avena barbata*, *Hordeum hystrix*, and *Lolium multiflorum*. In some localized areas, the vestiges of the old Pacific Bunchgrass region is seen in *Stipa pulchra* and the less common *Melica californica*. Some native *Trifolium*s are in abundance, particularly the striking *Trifolium barbigerum* var. *lilacinum* (Greene) Jepson.

*Agrostis tandilensis* is relatively inconspicuous in the beds and along the margins of these vernal pools, and often is masked by *Eryngium* and *Deschampsia danthonioides*. Sometimes, though, this grass is noticeable on the somewhat barren portions of the pools. The species generally is not abundant, and is certainly not a conspicuous element of its habitat. One or two pools were found supporting many plants of the

species, while most pools had none, or, if a few, the plants went unnoticed among other vegetation. In one pool the grass was associated with a related annual, *Agrostis microphylla* var. *intermedia* Beetle, remarkably distinctive from the pale green and shining panicles of *A. tandilensis* by its reddish panicles, but also easily overlooked among the ubiquitous *Deschampsia danthonioides*.—BEECHER CRAMPTON, Agronomy Herbarium, University of California, Davis.

CALIFORNIA BOTANICAL SOCIETY  
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Balance on hand in commercial account, January 15, 1956.....	\$ 464.15
From memberships and subscriptions.....	2,369.35
From sales of back numbers of <i>Madroño</i> .....	281.00
Receipts from annual dinner.....	170.50
Received as authors' share of publication costs.....	76.60
Contributions to endowment fund.....	2.50
Contributions to memorial fund.....	185.00
Total receipts .....	\$3,549.10

DISBURSEMENTS:

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Credited to endowment fund from contributions.....	2.50
Credited to memorial fund.....	185.00
Corresponding Secretary's expenses .....	62.15
Cost of annual dinner.....	163.08
Cancellation refunds .....	6.50
Cost of printing, binding, and mailing <i>Madroño</i> , Volume 13, Numbers 5, 6, 7, and 8.....	2,008.57
Total disbursements .....	\$2,708.80

BALANCE ON HAND IN COMMERCIAL ACCOUNT, American Trust Co., Palo Alto, January 15, 1957.....	\$ 840.30
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ENDOWMENT AND MEMORIAL FUND:

Palo Alto Mutual Savings and Loan Association, balance on hand January 15, 1957.....	\$3,998.72
Accrued interest .....	119.25
From sales of back numbers of <i>Madroño</i> .....	281.00
Contributions to memorial fund.....	185.00
Contributions to endowment fund.....	2.50
American Trust Company, savings account, balance January 15, 1957.....	\$ 372.58
Accrued interest .....	7.48
Total endowment .....	\$4,966.53

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June 6, 1957

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## DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See MADROÑO 9: 257-258. 1948.)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
COMPOSITAE				
<i>Aphanostephus arizonicus</i> A. Gray	n = 4	R. C. Jackson, UNM <sup>1</sup>	<i>Jackson 2059</i> , UNM	Bernalillo County, New Mexico
* <i>Engelmannia pinnatifida</i> Nutt.	n = 9	R. C. Jackson, UNM	<i>Jackson 2042</i> , UNM	Torrance County, New Mexico
<i>Gaillardia pinnatifida</i> Torr.	n = 17	R. C. Jackson, UNM	<i>Jackson 2033</i> , UNM	Bernalillo County, New Mexico
* <i>Haplopappus spinulosus</i> ssp. <i>typicus</i> H. M. Hall	n = 4	R. C. Jackson, UNM	<i>Jackson 2032</i> , UNM	Torrance County, New Mexico
* <i>Helianthus formosus</i> E. E. Watson	n = 51	R. C. Jackson, UNM	<i>Jackson 742</i> , IND	Marion County, Missouri
* <i>Hymenoxys argentea</i> (Gray) K. F. Parker	n = 15	R. C. Jackson, UNM	<i>Jackson 2038</i> , UNM	Bernalillo County, New Mexico
* <i>Melampodium leucanthum</i> Torr. & Gray	n = 10	R. C. Jackson, UNM	<i>Jackson 2082</i> , UNM	Bernalillo County, New Mexico
* <i>Psilostrophe tagetina</i> (Nutt.) Greene	n = 16	R. C. Jackson, UNM	<i>Jackson 2049</i> , UNM	Torrance County, New Mexico
CRUCIFERAE				
<i>Streptanthus amplexicaulis</i> (Wats.) Jeps.	n = 14	A. R. Krucke- berg, WTU	<i>Kruckeberg 1553</i> , WTU	San Gabriel Mountains, Los Angeles County, California
* <i>Streptanthus Howellii</i> Wats.	n = 14	A. R. Krucke- berg, WTU	<i>Kruckeberg 1881</i> , WTU	Siskiyou Mountains, Josephine County, Oregon

(continued on p. 112)

\* Prepared slide available.

<sup>1</sup> Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Second edition, 1954, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
LILIACEAE				
* <i>Fritillaria camtschatcensis</i> (L.) Ker-Gawl.	n = 12	R. Ornduff & A. R. Kruckeberg, WTU	Kruckeberg & Ornduff 4013, WTU	Stillaguamish River, Snohomish County, Washington
PORTULACACEAE				
* <i>Lewisia Tweedyi</i> (Gray) Robins.	n = 46	A. R. Kruckeberg, WTU	Kruckeberg 3320, WTU	Wenatchee Mountains, Chelan County, Washington
RANUNCULACEAE				
* <i>Delphinium bicolor</i> Nutt. forma <i>Helleri</i> (Rydb.) Ewan	n = 8	R. Ornduff, UC	Hitchcock & Muhlick 20781, WTU	About 20 miles east of Prineville on road to John Day, Crook County, Oregon
* <i>Nuttallianum</i> Pritz. ex Walpers	n = 8	R. Ornduff, UC	Hitchcock & Muhlick 20862, WTU	About 2 miles east of Plains, Sanders County, Montana
* <i>cyanoreios</i> Piper var. <i>cyanoreios</i>	n = 8	R. Ornduff, UC	Hitchcock & Muhlick 20820, WTU	About 18 miles south of Idaho City, Boise County, Idaho
			20835, WTU	About 21 miles west of Lowman, Boise County, Idaho
			20837, WTU	Two miles north of Cascade, Valley County, Idaho
* <i>cyanoreios</i> Piper forma <i>multiplex</i> Ewan	n = 8	R. Ornduff, UC	Hitchcock & Muhlick 20880, WTU	About 10 miles northwest of Ellensburg, Kittitas County, Washington

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Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954*).

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A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 4

OCTOBER, 1957

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# MADRÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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SOME AMERICAN SPECIES OF MARSILEA WITH SPECIAL  
REFERENCE TO THEIR EPIDERMAL AND  
SORAL CHARACTERS

K. M. GUPTA, D.Sc.

In connection with the monographic study of the genus *Marsilea* in India that has been undertaken in my laboratory at Jaswant College, Jodhpur, a loan of about one hundred and fifty sheets of *Marsilea* comprising eleven American species was received from the University of California Herbarium, Berkeley, for comparison with the Indian species. Of the species received, only two, *M. minuta* and *M. quadrifolia*, are represented in the Indian flora. Study of this material led to the paper here presented.

*Marsilea* is a genus of world-wide distribution. Just as *M. minuta* is of very wide occurrence in India from the Panjab in the north to Travancore in the south, *M. vestita* among the American species has a wide range of distribution throughout the western and Pacific United States and, like the Indian species, is very variable. It has been observed that *M. minuta* possesses varieties which are anatomically distinct, particularly in the internal organization of the sporocarps, but since this subject is now being studied by my research students from both the morphological and cytological point of view, I do not wish to anticipate their results herein. Miss Margaret Stason (1926), too, had hinted toward such a possibility while discussing the possible connection between *M. vestita* and *M. oligospora*. I should like to state that both these latter species seem distinct from one another.

Because the American material was limited in quantity, my study of these species is not as extensive as I would have liked. In some cases it was possible to remove only one or two sporocarps from the herbarium sheets for the study of their internal structures. However, the external characters were carefully studied and in spite of the fact that the genus is notorious for its morphological plasticity, one cannot always ignore certain differences like the shape of the leaflets (figs. 1-9) that might clearly be discernible among the allied species. I have, therefore, summarized these observations on the vegetative characters in Table 1.

On account of the limitations imposed for want of preserved material, I chose to remove only a few leaflets and some sporocarps from each of the collections in order to examine their epidermal and soral characters. It is a well known fact that with the publication of many important works on the epidermal and cuticular studies of vascular plants (Linsbauer, 1898; Porsch, 1905; Thomas and Bancroft, 1913; Rehfoos, 1917; Bandulska, 1923, 1926; Prat, 1932; Florin, 1931 and afterwards; Allsopp, 1952, 1953a, 1953b, 1953c, 1954, 1955), the taxonomic importance of such studies has gained world-wide significance. Linsbauer was probably

the first to study the epidermal characters in *Lycopodium*. Porsch had suggested the phylogenetic importance of stomatal characters, Rehfoos thought that the stomatal apparatus exhibits a constant feature within a group, and according to Miller (1938, p. 322) "the structure of the stomatal apparatus is markedly different in different groups of plants." Prat, after his comprehensive work on the epidermal structure of the Gramineae, stated that epidermal structures and their distribution of parts are specific characters. He says (1932, p. 185), "Correctement interprétés, les caractères épidermiques peuvent être de même valeur que les caractères qui ont servi de base à la définition des groupes systématiques." Satake (1934) has shown the systematic importance of the epidermal elements in the leaves of Japanese selaginellas and has founded a new classification on the basis of the epidermal structure of the leaves. Chowdhury (1937) studied the epidermis of eleven Indian species of *Lycopodium* and found that characters of the epidermis in most of the species were of diagnostic value. Some study has been made in my laboratory on the structure of the epidermis of some Indian species of *Selaginella*. As far as I know no detailed investigation on the epidermis of *Marsilea*, a plant with pronounced amphibious habit, has been undertaken in the past. The present examination, though brief, is clearly indicative of its usefulness.

The soral characters in the sporocarps of the genus have been studied in the past, but their systematic value had not yet been fully recognized.

**SPECIMENS EXAMINED.** The University of California material studied was collected by various workers over a period extending from 1849 to 1954. Except for *M. vestita*, which has a very wide distribution in the United States, all of the specimens examined are cited below:

**MARSILEA VESTITA** Hook. & Grev. UNITED STATES. Western Texas to El Paso, New Mexico, *Wright 811*, May-October 1849. UTAH. Rich County: Bear Lake near Laketown, *Porter 6490*, 30 June 1954. CALIFORNIA. San Diego County: *Purpus*, May-October 1898.

**MARSILEA MOLLIS** Rob. & Fern. MEXICO. CHIHUAHUA. St. Diego, *Hartman 604*, 20 April 1891. DURANGO. City of Durango and vicinity, *Palmer*, April-November 1896.

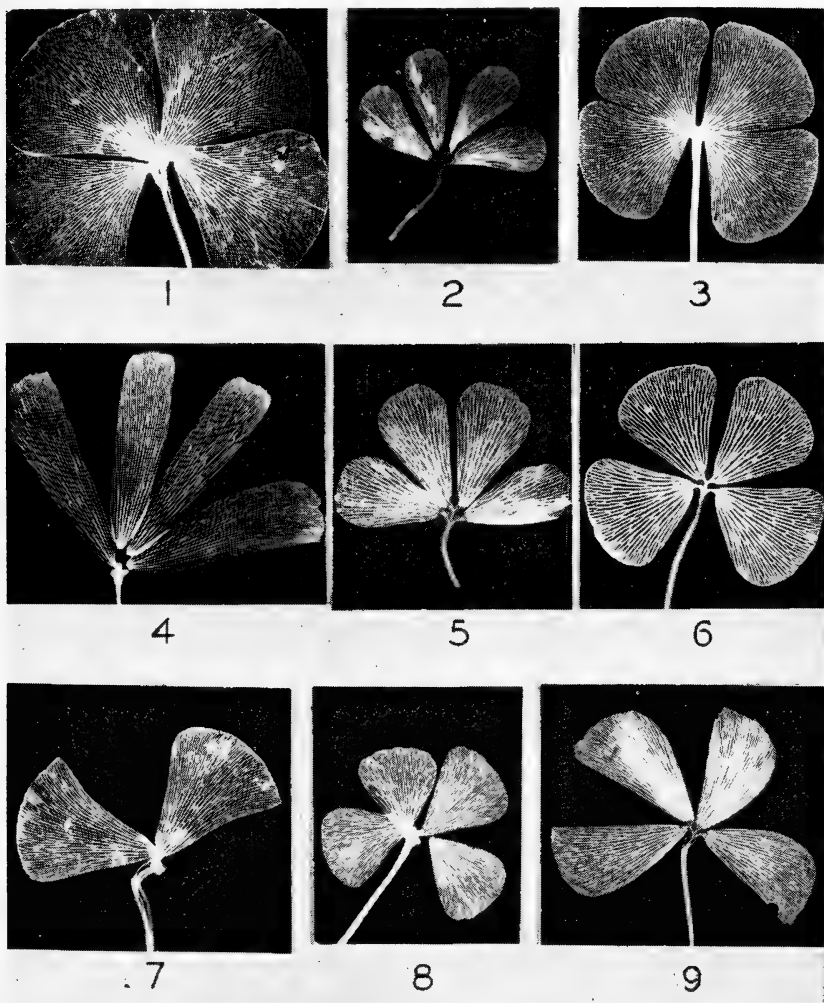
**MARSILEA MEXICANA** A. Br. MEXICO. CHIHUAHUA. Near Cusihiuriachic, *Pringle 2007*, 23 September 1888. SONORA. San Pedro, *Hartman 893*, 1894.

**MARSILEA MACROPODA** Engelm. MEXICO. TAMAULIPAS. Near Matamoras, *Pringle 1975*, 8 August 1888. UNITED STATES. TEXAS. (New Braunfels?), *Lindheimer 573*, 1846. Ponds on the Seco, *Reverchon 1630*, June, no year. Dimmit County: Turkey Creek south of Crystal City, *Muenschner & Winne 16506*, 29 June 1945. Jackson County: Lavaca River, *Tharp*, 29 August 1941.

**MARSILEA FOURNIERI** C. Chr. MEXICO. NUEVO LEON. Rio de San Juan outside of China, *Barkley 14344*, 27 February 1944. SONORA. Rancho San Carlos, 40 miles west of Hermosillo on road to Kino Bay, *Wiggins & Rollins 181*, 30 August 1941. BAJA CALIFORNIA. Seventeen miles south of Pozo Aleman, *Wiggins 7848*, 3 March 1935; 20 miles south of Calmalli, *Wiggins 5422*, 18 April 1931.

**MARSILEA UNCINATA** A. Br. UNITED STATES. Haven's Ranch, *Lemmon*, July 1882. TEXAS. Grown at Berlin Botanic Garden from fruit collected in Texas in 1872 by *E. Hall*. Comanche Spring, New Braunfels, *Lindheimer 1283*, June 1851. Caldwell County: dry sink, prairie, *Barkley 13130*, 7 July 1943.





FIGS. 1-9. Photographs of the quadrifoliate leaflets of *Marsilea* species, rendered transparent so as to show exact outlines and venation. 1, *M. cf. macropoda*,  $\times 0.8$ ; 2, *M. minuta*,  $\times 1.3$ ; 3, *M. mucronata*,  $\times 1.3$ ; 4, *M. tenuifolia*,  $\times 1.3$ ; 5, *M. mollis*,  $\times 2$ ; 6, *M. vestita*,  $\times 1.3$ ; 7, *M. uncinata* (lacking two leaflets),  $\times 2$ ; 8, *M. oligospora*,  $\times 1.3$ ; 9, *M. fournieri*,  $\times 1.8$ .

*MARSILEA TENUIFOLIA* Engelm. UNITED STATES. TEXAS. Inks Lake, *Tharþ*, 11 August 1941. (New Braunfels?), *Lindheimer* 745 in 1847. Llano County: creek near Kingsland, *Whitehouse* 18480, 4 May 1947; creek bed, *Tharþ*, 15 August 1940.

*MARSILEA OLIGOSPORA* Goodd. UNITED STATES. WYOMING. Uinta County: Jackson Lake, *Nelson* 6560, 12 August 1899 (isotype). Elmore County: King Hill, *Nelson & Macbride* 1158, 17 July 1911. Sublette County: near New Fork Lake, *Payson & Payson* 4437, 24 July 1925; Kendall, *Payson & Payson* 2920, 5 August 1922.

*MARSILEA MUCRONATA* A. Br. UNITED STATES. NORTH DAKOTA. Valley City,

*Stevens* 1223, 1 August 1950. Benson County: Butte, *Lunell*, 5 September 1905. NEBRASKA. Exeter, *Wibbe*, September 1888. WYOMING. String Lake, *Prettyman*, 20 July 1953.

MARSILEA QUADRIFOLIA L. UNITED STATES. CONNECTICUT. New Haven, *Setchell*, 3 October 1883. Cromwell, *Hubbard* 6817, no date. Litchfield County: Bantam Lake, *Bridgman*, 1888, *Thompson*, August 1891. MASSACHUSETTS. Falmouth, *Brooks*, 30 August 1910. Salem, *Harper & Harper*, 19 July 1895. Glacialis Pond, Cambridge, *Pease* 5672, 9 October 1904. Norfolk County: Wellesley, *Brown*, 14 August 1940. KENTUCKY. Fayette County: two miles east of Lexington, *McFarland* 46, 25 September 1940.

MARSILEA MINUTA L. MEXICO. COAHUILA. Cerro de Cypriano, *Purpus* 4525, July 1910. SINALOA. Culiacan, *Brandeggee*, 11 November 1904. BAJA CALIFORNIA. San Jose del Cabo, *Brandeggee*, September 1893, 16 October 1899, 25 October 1902. JALISCO. Near Guadalajara, *Pringle* 2434, 6 December 1889.

MARSILEA cf. MACROPODA Engelm. MEXICO. COAHUILA. Rancho Agua Bueno, 43 miles north of Monclova, *Gould* 6405, 20 June 1952.

In studying the above-cited specimens, the vegetative and reproductive structures were prepared in the following manner.

HAIRS. The hairs from different regions (leaves, nodes, and the sporocarps) were removed dry and mounted directly in liquid paraffin on a clean slide in the manner usually employed for the examination of fibers of wool or cotton, so as to bring out their medullated or non-medullated nature quite distinctly.

EPIDERMIS. For studying the epidermal structures, the leaves were treated with dilute KOH solution, washed in water, carefully teased, and stained with a single stain, safranin. After usual dehydration they were mounted in Canada balsam for examination.

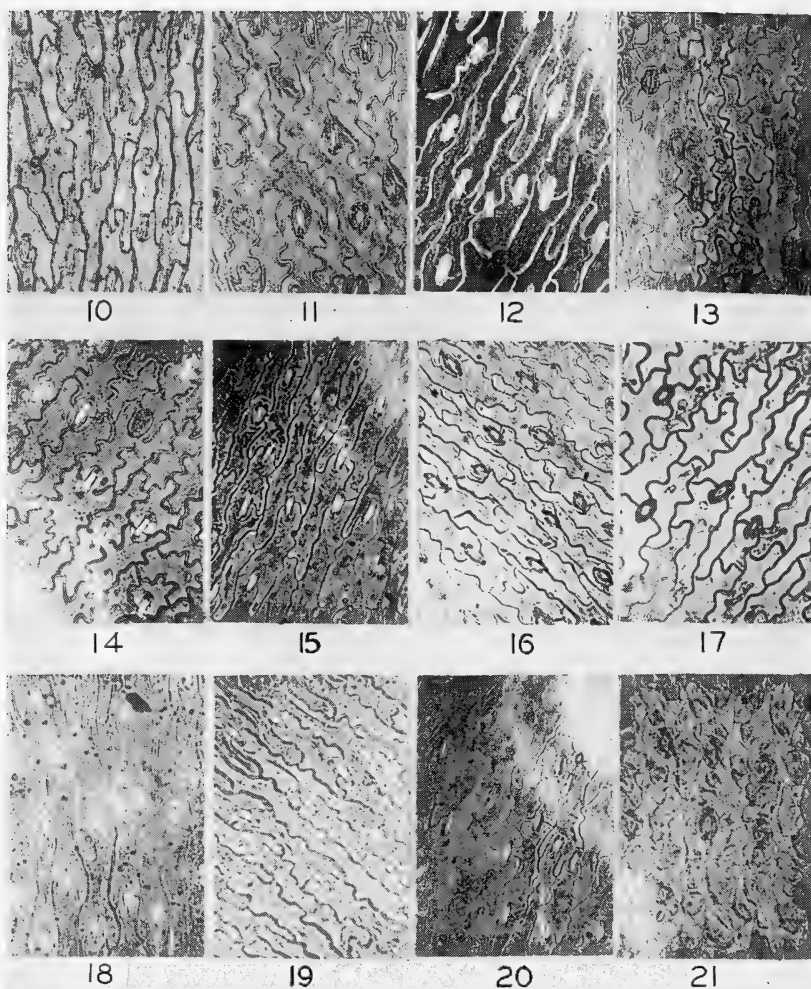
SPOROCARPS. The sporocarps were examined dry for their external features, but in order to ascertain their soral number, they were soaked in warm water after slightly scratching their resistant walls with a knife. This facilitated the so-called germination. The coming out of the mucilaginous mass is a mechanical process and cannot be strictly described as germination, as people often believe, because the real germination would mean the future activity of the mega- and microspores leading to the production of the gametophytes. The sporocarps were dissected further to study the nature of the sorus, the structure of the mega- and microsporangia, and also to find out whether the sporocarps were normal or possessed abnormalities which are often of a fluctuating type.

#### RANGE OF VARIATION

The habitats of *Marsilea* vary from aquatic to subterrestrial or terrestrial; almost all species start as aquatic plants during which time their vegetative growth is pronounced. Some, like *M. minuta*, also produce sporocarps in the aquatic habitat, while others, like *M. aegyptiaca*, never do so. The majority of the species possess the tendency to fruit only under a subterrestrial habitat, and in fact most of the specimens from the University of California Herbarium seem to have been collected under subterrestrial conditions. They grow in plains (100 feet above sea level) as

TABLE 1. VEGETATIVE CHARACTERS OF THE NORTH AMERICAN SPECIES OF MARSILEA

Name of species	General				Hairs				Epidermis			
	Habit	Length of petiole		Shape of leaflets	A/B Leaflet ratio	Average length in mm. and number of cells			Stomatal frequency	Size of stomata	Wall of epidermal cells	
		Min.	Max. Ave.			nodes	leaves	sporocarps				
M. vestita	Aquatic, sub-terrestrial and terrestrial	1.5	5.5	3.4	Obovate	0.33: 0.29	1.7; 7	1.4; 4	1.4; 7	22	0.02 x 0.01	Long, somewhat straight
M. mollis	Not mentioned	0.5	1.1	0.84	Cuneate	0.18: 0.08	-	1.0; 4	1.8; 5	10	0.03 x 0.02	Highly wavy
M. mexicana	Subterrestrial	5.0	6.3	5.6	Cuneate	0.33: 0.32	-	-	-	8	0.02 x 0.01	Less wavy
M. macropoda	Aquatic and subterrestrial	1.4	8.3	4.5	Obovate	0.39: 0.35	1.3; 9	1.9; 6	2.0; 9	9	0.03 x 0.01	Long and smooth
M. fournieri	Subterrestrial and terrestrial	1.0	2.4	2.69	Obovate	0.2: 0.14	2.9; 8	1.6; 5	1.3; 6	17	0.02 x 0.02	Long, narrow, wavy
M. uncinata	Terrestrial	1.1	3.0	2.45	Cuneate	0.24: 0.22	1.7; 7	0.5; 3	0.5; 5	13	0.02 x 0.01	Wavy
M. tenuifolia	Aquatic	2.5	6.3	3.79	Oblanceolate	0.94: 0.4	1.5; 10	0.6; 3	1.0; 5	6	0.03 x 0.01	Straight
M. oligospora	Aquatic and terrestrial	0.4	2.2	1.3	Obovate	0.24: 0.18	1.8; 8	1.1; 4	1.2; 6	6	0.02 x 0.01	Wavy
M. mucronata	Terrestrial	1.2	4.5	2.91	Cuneate	0.31: 0.23	0.3; 7	0.5; 3	0.5; 3	5	0.03 x 0.02	Wavy
M. quadrifolia	Aquatic, sub-terrestrial and terrestrial	2.6	11.1	4.34	Obovate	0.45: 0.41	1.5; 6	-	1.8; 6	5	0.02 x 0.01	Straight
M. minuta	Subterrestrial	1.5	6.0	3.4	Cuneate	0.29: 0.18	1.16; 7	0.9; 4	-	17	0.02 x 0.01	Wavy
M. cf. macropoda	Subterrestrial	10.6	14.0	12.6	Fan-shaped	1.04: 1.11	1.3; 8	2.0; 6	1.6; 6	8	0.02 x 0.01	Wavy



FIGS. 10-21. Photomicrographs of the epidermis of American Marsileas, showing nature of the epidermal cells and distribution of stomata. 10, *M. vestita*; 11, *M. oligospora*; 12, *M. macropoda*; 13, *M. cf. macropoda*; 14, *M. mollis*; 15, *M. mexicana*; 16, *M. fournieri*; 17, *M. uncinata*; 18, *M. tenuifolia*; 19, *M. minuta*; 20, *M. mucronata*; 21, *M. quadrifolia*. All about  $\times 85$ .

well as on mountains, 6000 feet or above. Not only this, but some species like *M. vestita* are found in the plains (160 feet above sea level) as well as in the higher altitudes (5800 feet), whereas a species like *M. mollis* is confined to higher levels (6000 feet) only.

The rhizome is creeping and branches dichotomously. The internodes are short or long, sometimes becoming very much reduced. The adventi-

tious roots, few or more in number in different species (one to eight), usually arise ventrally from the nodes of the rhizome. The size of the petiole varies considerably (from one to nine inches in length in different species), and so also the shape and size of the leaflets. The oblanceolate leaflets of *M. tenuifolia* (fig. 4) are quite peculiar to the species (Table 1).

The detailed examination of the structure of the hairs revealed the differences that exist among them in the different organs in the same species or on the same organs of the different species. The main point of interest is centered around the shape and size of either the basal or the terminal cells of the hairs of these organs (Table 1).

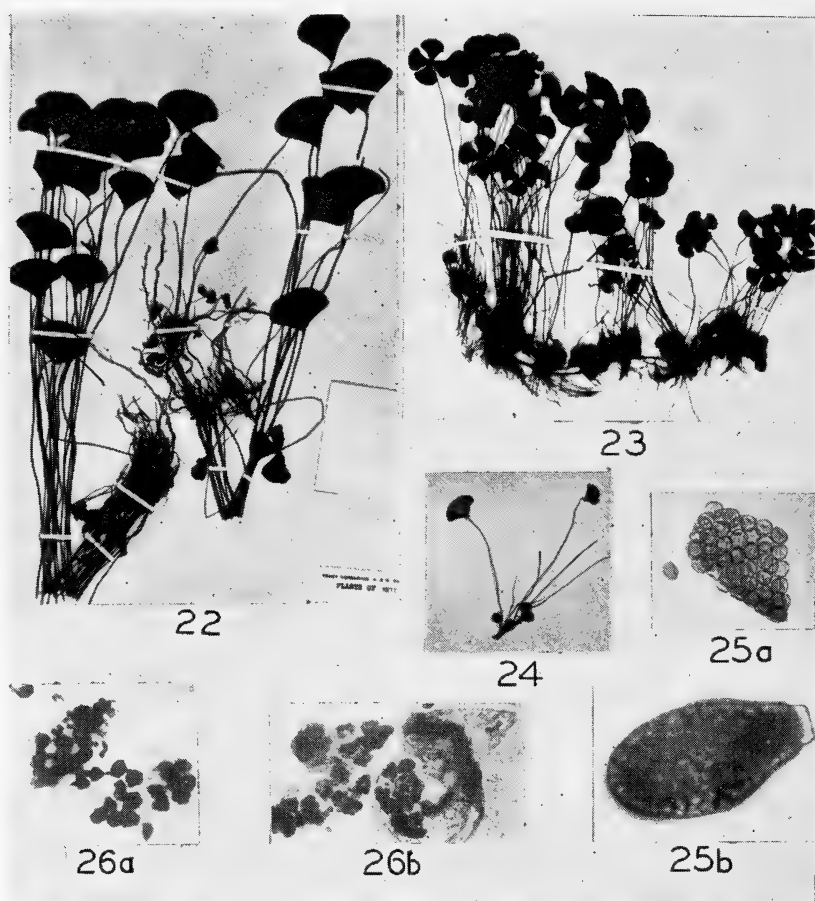
The study of epidermal structures has revealed that the species seem to differ from one another at least in two important respects, namely nature of the epidermal cells and the frequency of the stomatal distribution. The walls of the epidermal cells are either smooth, slightly wavy, or highly so, and the frequency of the stomata per unit area ranges from five to twenty (Table 1).

The sporocarps are stalked. Their attachment to the petiole is either basal or adnate, and the number of the sporocarps in a group may be one or more, connate or free (figs. 27–38). The shape differs from species to species, for instance it is subspherical in *M. minuta* (fig. 37), oval in *M. mollis* (fig. 28) and clearly bean-shaped in *M. vestita* (fig. 27). All the American species possess two horns, these varying in their prominence and bluntness. Similarly there is a difference in their soral number, a fact that seems to be of some systematic importance in the genus *Marsilea*.

#### DISCUSSION OF THE SPECIES

MARSILEA VESTITA and M. OLIGOSPORA. *Marsilea vestita* is very well represented in the collection by 84 sheets which date from 1894 to 1954. While the general characters are given in tables 1 and 2, I should like to mention a few interesting observations on this species. The anatomy of the epidermis shows that the walls of the epidermal cells are long and more or less straight (fig. 10). The stomata are uniformly distributed throughout, their orientation being in the direction of the length of the epidermal cells. The frequency of the stomatal distribution is almost the highest among the species here examined, namely twenty-two per unit area.

There is a single stalked sporocarp in *M. vestita* which is attached at the base of the petiole. It is bean-shaped and possesses both the horns, the upper pointed and the lower one blunt (fig. 27). An abnormal specimen with a sporocarp adnate to the petiole was found on sheet UC 205105 (fig. 24). Most of the specimens possessed normal sporocarps with normal type of both mega- and microspores (figs. 25a, 25b), but a critical search of the specimens revealed the presence of abnormal sporocarps (fig. 26a). The latter had no megaspores but only microspores. Sometimes these microspores were also of two types (fig. 26b). As pointed out in the



FIGS. 22-26. FIG. 22, *M. cf. macropoda*, habit showing largest leaflets and petioles, ca.  $\times 0.25$ . FIG. 23, *M. macropoda*, same for comparison, ca.  $\times 0.25$ . FIG. 24, *M. vestita*, abnormal specimen found on UC 205105, sporocarp adnate to petiole,  $\times 0.25$ . FIG. 25, *M. vestita*, megaspores (25b) and microspores (25a) from a normal sporocarp,  $\times 25$ . FIG. 26, *M. vestita*, microspores from two different sporocarps (26a, abnormal; 26b, normal),  $\times 25$ . Generally in abnormal sporocarps megaspores are absent.

introduction, such a thing was expected in a species with a wide distribution; however, the significance of these and such other abnormal sporocarps as have been discovered in more than one Indian species is not discussed here.

It is important to point out that Miss Stason's observation (1926, p. 478) that *M. oligospora* may be an "ecotype" of *M. vestita* may not be quite correct, for I find that the epidermal as well as soral characters are distinct in the two species (figs. 10, 11, 27, 34) insofar as they are repre-

sented in the collection studied. For these reasons I prefer to regard *M. oligospora* as a distinct species rather than just an ecotype of *M. vestita*.

MARSILEA MACROPODA and *M. cf. MACROPODA*. Five sheets in the series studied represent *M. macropoda* (fig. 23) and one specimen is questionably referred to that taxon as *M. cf. macropoda* (fig. 22). At the outset I should like to mention that these two look quite distinct from one another. The latter possesses not only larger leaves and sporocarps than *M. macropoda*, but probably larger than any species (figs. 1–9) represented in the series here treated. The epidermal cells in *M. macropoda* possess long and smooth walls (fig. 12), whereas in *M. cf. macropoda* the epidermal cells possess wavy cell walls (fig. 13) with stomatal frequency, however, being nearly the same in the two cases, namely nine and eight, respectively.

The sporocarps are stalked and tufted at the base of the petiole in *M. macropoda* (fig. 30). They are oval in shape and the biggest in size as compared with other species. On the other hand a group of only two or three sporocarps which are slightly adnate to the petiole is found in the specimens of *M. cf. macropoda* (fig. 38). The sporocarps in the two cases are, however, densely covered with hairs and possess both the horns, the lower one being more prominent.

One of the petioles in *M. macropoda* bears five leaflets instead of the usual four. This is not a very unusual feature in Marsileas, having been described for *M. quadrifolia* in 1948 and *M. aegyptiaca* in 1956.

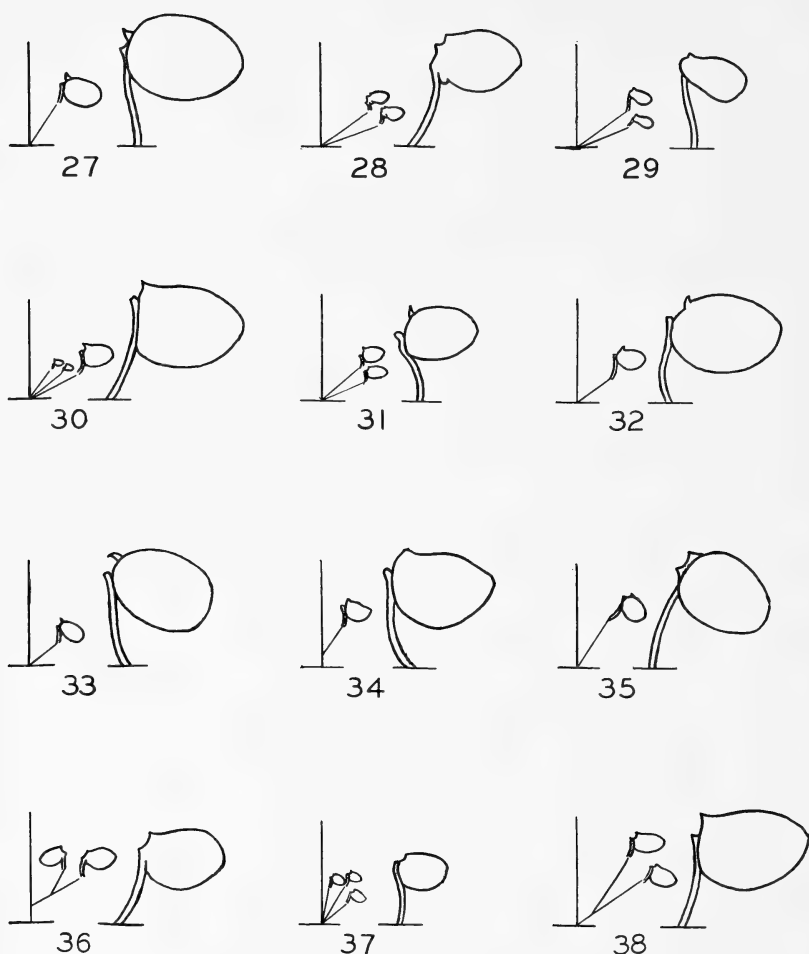
MARSILEA MOLLIS. There is only one herbarium sheet of this species, containing plants collected at two different times (1891 and 1896). The habit of this species is quite characteristic, with small hairy leaflets. There are no rhizomes or roots preserved; perhaps these are very much reduced. The epidermal cells of the leaves show wavy nature in their walls (fig. 14) and the uniformly distributed stomata show a frequency of about ten stomata per unit area.

The stalked sporocarps are tufted in nature, and their exact mode of attachment is not possible to describe in the absence of the rhizomes. The hairy and ribbed sporocarps are more or less oval in shape and possess two blunt horns (fig. 28). The soral number is about 15 in the species.

MARSILEA MEXICANA. The two herbarium sheets of this species (collected in 1888 and 1894) are badly preserved. The leaves show epidermal cells which are less wavy and possess stomatal frequency of only eight per unit area (fig. 15).

The sporocarps are a bit characteristic in being somewhat narrower on the sides and swollen in the middle (fig. 29). They are ribbed and possess two blunt horns, with soral number twelve.

MARSILEA FOURNIERI. The four herbarium sheets contain material from both subterrestrial and terrestrial habitats. The leaves are obovate. The epidermal cells are long and narrow with their walls wavy in nature (fig. 16). The stomatal frequency is quite high, as much as 17 per unit area.



FIGS. 27-38. Outline diagrams showing attachment of sporocarps to the petiole and the peduncles as well as the shape of the individual sporocarps. 27, *M. vestita*; 28, *M. mollis*; 29, *M. mexicana*; 30, *M. macropoda*; 31, *M. fournieri*; 32, *M. uncinata*; 33, *M. tenuifolia*; 34, *M. oligospora*; 35, *M. mucronata*; 36, *M. quadrifolia*; 37, *M. minuta*; 38, *M. cf. macropoda*. All about  $\times 30$ .

The stalked sporocarps remain tufted at the base of the petiole. They are clearly bean-shaped and possess both the horns, which are pointed. The upper horn is further characterized by being longer and curved (fig. 31). The ripe mature sporocarps are quite smooth and ribbed, otherwise the species, like *M. macropoda*, is profusely covered with hairs.

**MARSILEA UNCINATA.** In the four herbarium sheets the vegetative characters are quite variable, as for instance the number of roots (2 to 8) on



the nodes and the size of the internodes. The leaves are cuneate, possessing epidermal cells with wavy walls (fig. 17). The stomatal frequency is thirteen per unit area.

There is a single stalked sporocarp which is oval in shape and is attached almost at the base of the petiole. There are two horns present on the sporocarp, the upper one being pointed and curved (fig. 32). The pedicel is fully adnate to the body of the sporocarp, which is smooth and possesses 16–18 sori.

*MARSILEA TENUIFOLIA*. The four herbarium sheets all contain material collected in an aquatic habitat. The leaves are very characteristic of the species, being oblanceolate in shape (fig. 4). The anatomy of the epidermis shows that the epidermal cells are long and narrow. The walls of the epidermal cells are smooth (fig. 18). The distance between the two walls of the same epidermal cell is narrow in the non-stomatal region and increases in the stomatal region as if to house the stomata. The frequency of stomatal distribution is 6 per unit area.

The single bean-shaped sporocarp is attached by a short stalk at the base of the petiole. There are two horns present; the upper one is pointed and curved downwards (fig. 33); the wall of the sporocarp is smooth and not hairy. It may be noted that there were only two sporocarps present on one specimen, while other plants were sterile.

*MARSILEA MUCRONATA*. The four herbarium sheets were all collected from a terrestrial habitat. The leaflets are cuneate in shape. The anatomy shows epidermal cells with wavy cell walls (fig. 20). The frequency of stomatal distribution is lowest in this species, being only five per unit area.

The sporocarps are usually solitary, rarely two arising from the base of the petiole. They are bean-shaped with the pedicels partially adnate to the sporocarps (fig. 35). There are two horns; both are pointed. The soral number is 16.

*MARSILEA MINUTA* and *M. QUADRIFOLIA*. Both these species are found widely distributed in India and are the common ones that have been described previously in and outside India (Pande, 1923; Mahabale & Gorji, 1948; Mehra, 1938; Puri & Garg, 1953; and Williams, 1920). And as a further study of the Indian species is in hand, it is not profitable to deal with them here, particularly in view of the fact that the University of California specimens did not contain enough material of well preserved nature.

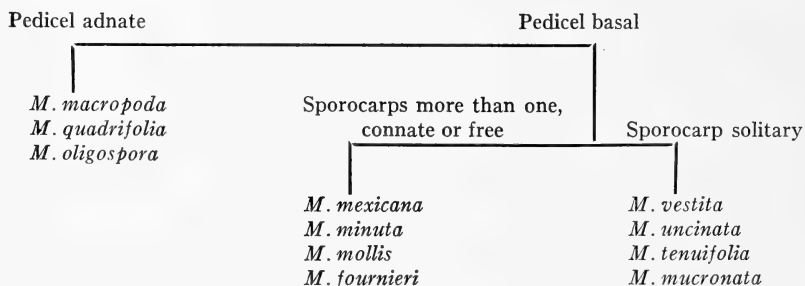
The epidermal studies (figs. 19, 21) in both the species have revealed that the stomatal frequencies in these are different, being five in *M. quadrifolia* and seventeen in *M. minuta*. Similarly the attachment of the sporocarp is characteristic in *M. quadrifolia*, being adnate to the petiole and connate to the pedicel (fig. 36), while in *M. minuta* two to six sporocarps are slightly connate at the base of the petiole (fig. 37). The comparison with the Indian material available in my laboratory indicated minor differences, but, in view of wide distribution of these species, these minor differences are natural.

## CONCLUSION

From the foregoing brief description of eleven American species of *Marsilea*, it is apparent that the genus exhibits clear variations in the vegetative as well as in the reproductive organs, namely the sporocarps. In spite of a similar habitat, whether aquatic, subterrestrial or terrestrial, species do differ from one another, say for instance in the shape and size of their leaves (figs. 1–9) and structures of their sporocarps (figs. 27–38). The other types of variations that are often present in the same species under varied environmental conditions are distinctly different from the former differences, and are always exhibited within certain limits in that species. The latter should not be confused with the former. A thorough ecological study, therefore, becomes imperative, besides other important considerations of anatomy and cytology, not only to decide clearly the differences between two species but also to find out the range of variations within the species. Such an autecological aspect is being attempted with *M. aegyptiaca* here in the Botany Department at Jaswant College.

One simple aspect of morphology, namely the examination of the epidermis of the leaflets of these eleven species of *Marsilea*, has demonstrated how the structure of the walls of the epidermal cells and the frequency of stomatal distribution can be of some diagnostic value. It has been possible to indicate in the present thesis, for instance, that the species pairs *M. vestita*–*M. oligospora* and *M. macropoda*–*M. cf. macropoda* are quite distinct. If only the two above characters of the epidermis are taken into consideration, the present collection can be arranged into three different categories, namely, those with wavy walls, those with less wavy walls and those with smooth walls.

The structure and attachment of the sporocarps, however, provide the main clue to the correct identification of the species. The main features that are useful and essential for systematic considerations have been mentioned in Table 2. For the present, however, the number of sporocarps in a group and the nature of attachment of these sporocarps to the petiole have been adopted as a broad basis for classification (Gupta & Bhardwaja, 1956). Accordingly these American species can be arranged as follows:



It must, however, be admitted that the systematics of the genus *Marsilea* is a neglected subject, and it is hoped that as a result of detailed

TABLE 2. MORPHOLOGICAL CHARACTERS OF THE SPOROCARPS IN THE AMERICAN SPECIES OF MARSILEA

Name of species	Disposition	External				Internal			
		Relation of pedicel to petiole	Relation of pedicel to pedicel	Shape and size	Attachment of pedicel to sporocarp	Nature and number of horns	Soral number	Megasporangia and spores	Microsporangia and spores
<i>M. vestita</i>	Solitary	At the base	Free	0.18 Bean-shaped	Fully adnate	2, upper horn pointed	18	Normal or absent	Normal or abnormal
<i>M. mollis</i>	Tufted (?)	At the base	Not seen	0.11 Oval-shaped	Partially adnate	2, blunt	14-15	Normal	Normal
<i>M. mexicana</i>	Tufted	At the base	Partially connate, free (?)	0.11	Partially adnate	2, blunt	12	Normal	Normal
<i>M. macropoda</i>	Tufted	Slightly adnate at the base	Slightly connate at the base	0.25 Oval-shaped	Fully adnate	2, lower prominent	20	Normal	Normal
<i>M. fourieri</i>	Tufted (?)	At the base	Slightly connate at the base	0.11 Bean-shaped	Fully adnate	2, both pointed upper one slightly curved towards right	17	Normal	Normal
<i>M. uncinata</i>	Solitary	At the base	Free	0.13 Oval-shaped	Partially adnate	2, upper more pointed and more curved towards right	16-18	Normal	Normal
<i>M. tenuifolia</i>	Solitary	At the base	Free	0.13 Bean-shaped	Fully adnate	2, same as above	-	Normal	Normal
<i>M. oligospora</i>	Solitary rarely two	Slightly adnate at the base	Free	0.16 Oval-shaped	Partially adnate	2, lower more prominent, upper obscure	14	Normal	Normal
<i>M. mucronata</i>	Solitary rarely two	At the base	Free	0.2 Oval-shaped	Partially adnate	2, both pointed	16	Normal	Normal
<i>M. quadrifolia</i>	2, 3	Adnate	Connate	0.14 Oval-shaped	Fully adnate	2	16-20	Normal	Normal
<i>M. minuta</i>	2, 3	At the base	Free	0.11 Subspherical	Fully adnate	2	13	Normal	Normal
<i>M. cf. macropoda</i>	2, 3	Slightly adnate	Connate	0.21 Oval-shaped	Fully adnate	2, lower prominent			

investigation that is proceeding in the Botany Department at Jaswant College, some useful light will be thrown on the problem. Ecological, morphological and cytological studies of some Indian species seem to indicate a very promising field, and it may be possible in the near future to throw light on the nature of various so-called "ecotypes" possessing fertile or fluctuating type of sterile sporocarps, as a matter of fact, on the entire phenomenon of speciation in the genus *Marsilea*.

#### SUMMARY

Herbarium specimens representing eleven different species of *Marsilea* from North America have been examined, and in each case the structure of the epidermis and the sporocarps has been described. It has been shown that the species differ from each other in nature of their epidermal cells and the distribution of their stomata. So also they differ in external and internal characters of their sporocarps. The more important characters of the latter, as well as vegetative features in all these species, have been tabulated; in addition, the anatomical features of the leaves have been given in a series of photographs to indicate clearly that vegetative features, both external and internal, do contribute minor, if not major, criteria in identification of the various species of *Marsilea*.

#### ACKNOWLEDGMENTS

For the loan of the material of these American species of *Marsilea*, I am extremely grateful to Professor H. L. Mason, Director of the University of California Herbarium, and especially for his great kindness in allowing me to remove parts of the plants from the herbarium sheets for investigation, and for permitting me to keep the entire collection at Jodhpur for more than a year.

It is my pleasure to record the assistance given me by my two pupils, Shri T. N. Bhardwaja, M.Sc. and P. L. Mital, M.Sc., in preparing this paper for publication. My thanks are also due to my laboratory staff for their help in the preparation of the manuscript.

Jaswant College  
Jodhpur, India

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CHROMOSOME COUNTS IN THE SECTION *SIMIOLUS* OF THE GENUS *MIMULUS* (SCROPHULARIACEAE). II.

BARID B. MUKHERJEE, DELBERT WIENS, AND ROBERT K. VICKERY, JR.

This cytological study<sup>1</sup>, which is a continuation of a previous investigation of chromosome numbers in section *Simiolus* (Vickery, 1955), forms an integral part of a long range experimental study of the taxonomy, cytogenetics, and evolution of species in the genus *Mimulus* (Vickery, 1951). The counts were determined from observation of various stages of microsporogenesis. Many different techniques of fixation and staining were tried in an attempt to develop a better method than the one previously used (Vickery, 1955).

An effective and comparatively simple method was developed for obtaining chromosome counts. Buds of proper size, which varied from 1.6 to 3.1 millimeters, were killed and fixed for about two hours in a mixture of one part acetic acid to two parts distilled water. Buds that could not be studied immediately were stored in 70% ethanol. The best time for fixation proved to be from 9 to 11 a. m. The anthers were dissected out of the buds and stained in strong aceto-carmine. The stain was prepared by dissolving 1 gram of carmine in 100 mls. of boiling 45% acetic acid. It was cooled and filtered before use. The anthers were placed in a drop of stain on a microscope slide and heated gently over an alcohol flame. A cover slip was added and pressed firmly with a match stick to squash the anthers. From time to time during the next half hour more stain was added, more pressure applied and more heat used. The excess stain was removed with a paper towel pad. The coverglass was sealed with a half and half mixture of beeswax and paraffin. In a few cases propionic acid was substituted, with equally satisfactory results, for acetic acid in the above schedule.

The slides were examined within a day or two and the best figures found were drawn with the aid of a camera lucida (fig. 1). The method of Bhaduri and Ghosh (1954) was employed to make the slides permanent but with only moderate success. Herbarium specimens of all the cultures counted have been prepared for future reference and will be deposited in the Garrett Herbarium of the University of Utah under the culture numbers given in Table 1.

The chromosome numbers were found to be  $n=16$  for *M. dentilobus* Rob. & Fern. from Chihuahua, Mexico,  $n=15$  for *M. glabratus* var. *utahensis* Pennell from southern Utah, and  $n=14$  for the ten cultures of *M. guttatus* DC. from California and northern Utah. These taxa appear to form an aneuploid sequence and a geographic series linking a group of North American taxa reported as  $n=14$  (Campbell, 1950, and Vickery,

<sup>1</sup> The work was supported by grants from the National Science Foundation and the University of Utah Research Fund. The authors wish to thank Drs. W. W. Newby and C. M. Woolf for their helpful criticisms of the manuscript.

Table 1. CHROMOSOME COUNTS IN MIMULUS, SECTION SIMIOLUS

n = 16	<i>M. dentilobus</i> Rob. & Fern. Sierra Charro, Chihuahua, Mexico. <i>Gentry</i> 8073 (5324).
n = 15	<i>M. glabratus</i> var. <i>utahensis</i> Pennell. Fremont River, Bicknell, Wayne County, Utah, altitude 7100 feet, <i>Vickery</i> 600 (5265).
n = 14	<i>M. guttatus</i> DC. Mono Inn, Mono County, California, altitude 6420 feet, <i>Clausen</i> 2043 (5015).  Darwin Falls, Inyo County, California, altitude 2500 feet, U. C. Herbarium 696020 (5017).  Mt. Diablo, Contra Costa County, California, altitude 1000 feet, <i>Stebbins</i> 703 (5052).  Mt. Oso, Stanislaus County, California, altitude 1000 feet, <i>Vickery</i> 190 (5346).  Bountiful, Salt Lake County, Utah, altitude 4800 feet, <i>Vickery</i> 331 (5835).  Mill Creek Canyon, Salt Lake County, Utah, altitude 5800 feet, <i>Vickery</i> 335 (5840).  Alta, Salt Lake County, Utah, altitude 8800 feet, <i>Vickery</i> 336 (5845).  Kimball Junction, Summit County, Utah, altitude 6600 feet, <i>Vickery</i> 341 (5856).  Hailstone, Wasatch County, Utah, altitude 6300 feet, <i>Vickery</i> 342 (5857).  Rock Creek, below Davies Resort, Duchesne County, Utah, altitude 7600 feet, <i>Del Wiens</i> 8/5/56 (5968).

1955) with a group of South American taxa reported as  $2n=32, 48$ , and ca. 64 by Sugiura, Maude, and Brozek, respectively (Darlington and Wylie, 1955). However, the distinctive morphological characteristics of *M. dentilobus* (Grant, 1924) suggest to the authors that it is not a link in this aneuploid series and is not closely related to any of the North or South American species of *Mimulus*. Furthermore, interspecific crosses (Vickery, 1956) indicate that *M. dentilobus* is genetically isolated from all the other taxa of its section. Therefore, it appears to be an evolutionary side-shoot from the main group of *Simiolus* species. On the other hand, the morphology of *M. glabratus* HBK., which is the only species of the section common to North and South America, indicates relationships to both the North and South American groups of species. An  $n=14$  culture of *M. glabratus* var. *utahensis* (5048) hybridizes with members of the various taxa of the two groups although the hybrids are nearly sterile (Vickery, 1956). Therefore, in view of the possible evolutionary role of *M. glabratus* as a connecting link between the North and South American taxa

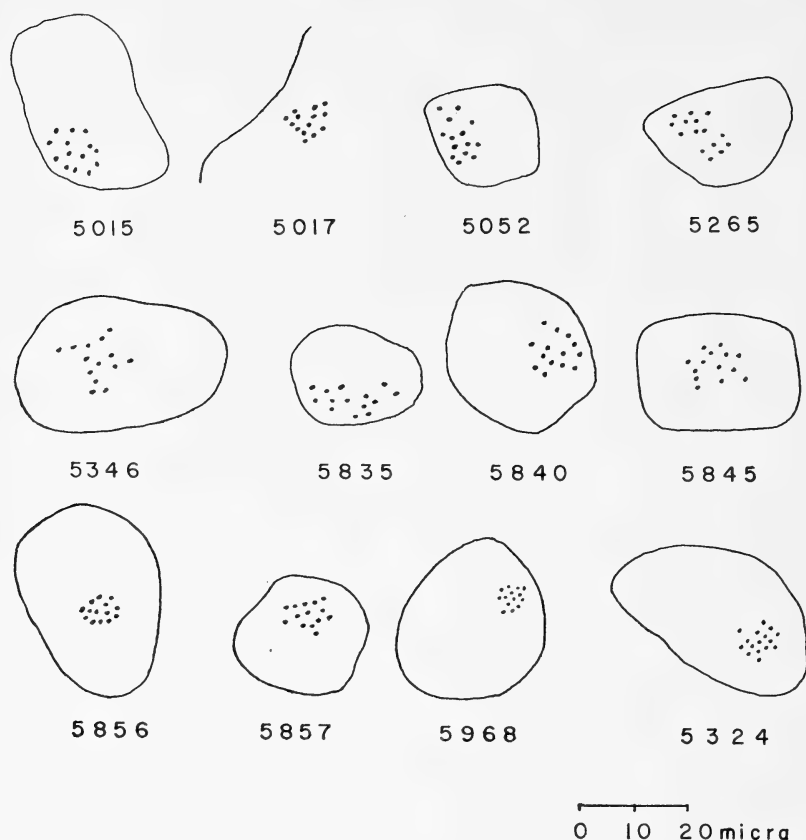


FIG. 1. Meiotic chromosomes of pollen mother cells of *Mimulus*,  $\times 750$ . All drawings were made with the aid of a camera lucida. The numbers below the figures are the culture numbers (Table 1). The ten cultures of *M. guttatus* are  $n=14$ . The one culture of *M. glabratus* var. *utahensis* (5265) is  $n=15$ . *M. dentilobus* (5324) is  $n=16$ . All plants are in first metaphase except 5015, 5968, and 5324 which are in second metaphase.

of section *Simiolus*, the aneuploid number of  $n=15$  for the Bicknell culture (5265) of *M. glabratus* var. *utahensis* is particularly interesting and significant. Further work is in progress to be sure that this count does not represent merely an aberrant individual.

The extensive hybridization experiments mentioned above (Vickery, 1956) reveal crossing barriers of various degrees between the different cultures of *M. guttatus*. However, in no case is a culture completely isolated from all the others. The results of these crosses suggested to the authors that all the cultures of the races of *M. guttatus* would have the



same chromosome number. Our cytological observations confirm this idea and suggest, further, that the crossing barriers are due not only to gene differences but also to differences in chromosome structure. For example, culture 5968 has markedly smaller chromosomes than the other cultures. Probably there are cryptic structural differences in the chromosomes of the cultures as well.

In conclusion, we may report that our studies indicate that the North American *M. guttatus* complex of species ( $n=14$ ) appears to be related to the South American *M. luteus* complex ( $x=8$ ) by a series of aneuploid forms of *M. glabratus*. Work is in progress to determine the chromosome numbers of additional taxa and to determine the chromosomal homologies of the various cultures and races in order to clarify further our understanding of the evolutionary relationships in the group.

Department of Genetics and Cytology  
University of Utah  
Salt Lake City 12, Utah

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## ON THE SPECIFIC DISTINCTNESS OF RUDBECKIA LACINIATA AND R. AMPLA

GEORGE NEVILLE JONES

Wild goldenglow, *Rudbeckia laciniata* L. (Sp. Pl. 906, 1753), is a rather familiar plant growing in alluvial soil in eastern United States and adjacent Canada, ranging from Quebec to Manitoba and southward to eastern Texas and Florida. A morphologically similar plant described from Colorado in 1901 as *R. ampla* A. Nels., occurring in the western parts of the continent from Saskatchewan to South Dakota, New Mexico, Arizona, and Idaho, is less well known, and generally has been treated by contemporary students of the western flora as a synonym of *R. laciniata*.

There is evidence, however, on the basis of study of morphological characters, habitat, and habit, as well as geographical distribution, that

these plants represent different taxa, apparently two distinct species. An alternative interpretation is that *R. ampla* might be treated as a "variety" or subspecies of *R. laciniata*, as the historical trend of human migration had led to discovery and publication of the latter taxon 148 years earlier. However, if one of them should be regarded as a subspecies of the other, the reverse process of designating *R. laciniata* as a subspecies of *R. ampla* is for certain reasons indicated as the more logical course.

According to a theory of origin of the genus *Rudbeckia* expressed by W. M. Sharp (Ann. Mo. Bot. Gard. 22:60. 1935), the present species are descended from an ancestral group originating on the Appalachian or the Ozarkian upland regions exposed since the close of the Paleozoic, the most recent of them inhabiting the Coastal Plain from Virginia to Texas. From this it would appear that *R. laciniata* and *R. ampla*, although morphologically similar, may have had different origins, the latter being much older, and the former of relatively recent origin on or near the Coastal Plain. It would be illogical to treat *R. ampla* as a subspecies of *R. laciniata* simply because the latter was discovered first. It seems therefore most practical to continue to designate each of them by a binary name. This procedure serves to express relationship satisfactorily, and there is no need for "new combinations" or other nomenclatural change.

Some of the diagnostic characters of these two species are summarized in the following key:

Heads ("disk") 1.5–2 cm. in diameter, becoming ellipsoid and 3–4 cm. in length; rays 9–15 mm. wide; disk corollas 5 mm. long; achenes 5–6 mm. long; receptacular bracts ("chaff") linear, 6–7 mm. long; pappus coroniform, the teeth short, obtuse, indistinct or none; leaves glabrous beneath, the upper surface somewhat strigose toward the apex of the leaf, the trichomes with enlarged pustular bases; basal leaves palmately ternate with broad segments and narrow sinuses; plants 1–1.5 m. tall; peduncles few, stout (1.5–3 mm. thick below the head)....*R. ampla*

Heads ("disk") globose, 1–1.5 cm. in diameter; rays usually less than 1 cm. wide; disk corollas 3–4 mm. long; achenes 3–4 mm. long; receptacular bracts spatulate, 3–4 mm. long; pappus crown of 4 teeth; upper leaves glabrous above, usually finely strigose beneath varying to nearly glabrous; basal and lower cauline leaves pinnately divided into relatively narrow segments with wide sinuses; plants 1.5–3 m. tall; peduncles several, slender (about 1 mm. thick below the head)

*R. laciniata*

The relevant bibliographical references to *R. ampla* follow. It is not necessary to list here the extensive bibliography of *R. laciniata* L.

*Rudbeckia ampla* A. Nelson, Bull. Torrey Club 28: 234, 1901; Rydberg, Fl. Colorado 371, 1906, Fl. Rocky Mts., 927, 1917, Fl. Pr. & Pl. 836, 1932. *Rudbeckia laciniata* sensu A. Gray, Syn. Fl. 1(2): 262, 1878, ex parte; A. Nelson, Man. Bot. Rocky Mts. 544, 1909; Kearney & Peebles, Flowering Pl. Arizona 950, 1942, Arizona Flora 898, 1951; Davis, Fl. Idaho 777, 1952; Weber, Handb. Pl. Colorado Front Range 194, 1953; Harrington, Man. Pl. Colorado 598, 1954; non L., 1753.

Type locality. Colorado. The first cited specimen is *Baker 699* from Pagosa Springs.

To those who may be familiar with these plants the habit and appearance of members of the two taxa are noticeably different, although, as often happens in descriptive taxonomy, some of the differences are not easily stated in objective terms. In general, however, *Rudbeckia ampla* is a shorter, somewhat stouter plant with larger heads on fewer and stouter peduncles, the rays averaging somewhat wider. The disk corollas, achenes, and receptacular bracts are longer, the latter, commonly known as "chaff," furnishing distinctive characters that have been found to be important in the taxonomy of other species of the genus. Finally, it may be pointed out that the pappus of *R. ampla* is more coroniform, and the leaves are usually thicker and with different indument. In some specimens of *R. laciniata* the undersurface of the leaves tends to be less pubescent than in others, but almost all leaves show at least a few trichomes, particularly when viewed under the binocular microscope. It may be appropriate to note here that some published statements concerning *R. laciniata* are perhaps not as explicit as they should be. Unless modified, they may serve as a barrier to clarity of understanding of the plants described. For example, in the eighth edition of Gray's Manual the statements referring to the elongation of the "disk" of *R. laciniata*, as well as that indicating length of achenes, appear to be somewhat exaggerated, and are more nearly applicable to *R. ampla*.

Department of Botany,  
University of Illinois, Urbana

## PINES FROM NUEVO LEON, MEXICO

BRUCE ZOBEL AND FRANKLIN CECHE<sup>1</sup>

The forest geneticist usually attempts to grow as many as possible of the different strains and species of trees in which he is interested. These may be used for two purposes: 1) to establish a breeding arboretum, the trees to be used as parents for desired crosses; 2) to establish, on a limited scale, trials of adaptability to local or special environmental conditions. Both purposes were in mind when the Texas Forest Service sponsored two pine collection trips to the state of Nuevo León, Mexico. In conjunction with drought resistance studies, species that can do well under severe conditions of heat and drought were especially sought.

The accrual of further knowledge of the taxonomic and evolutionary position of the Mexican pines was another objective of importance. The purpose of this paper is to report on the several pine species and their many intergrading forms found growing in one of the states of northeastern Mexico, Nuevo León. Although collections were not made at all points in the state, the three areas visited were intensively studied, and

<sup>1</sup> Silviculturist and Assistant Silviculturist, respectively, Texas Forest Service.



FIG. 1. Southern end of Nuevo León showing major area from which collections were made. The other two collecting areas were at more northerly points in the state.

complete records, specimens, and photographs were obtained for each species encountered.

The collection trips were the direct result of an invitation sent by Dr. E. A. Pequeño, Director, Instituto de Investigaciones Científicas, Universidad de Nuevo León. Though not a forester, Dr. Pequeño has an intense interest in the research upon and wise use of Mexico's forest resources, for he is fully cognizant of what their destructive exploitation will do to the economy of the country.



FIG. 2. Vicinity of La Encantada, illustrating the type and extent of the virgin forests in this area. A true fir (*Abies*) is in foreground.

The first trip was made in late September, 1954, with the senior author accompanied by Mr. Ruben Rocha, a Mexican student at Agricultural and Mechanical College of Texas, who acted as interpreter. This trip was preliminary in nature and little actual material was collected, because few pines bore cones that fall. However, many yearling cones indicated the possibility of a large cone crop for the following year. It was determined on this first trip that although a few species of pines matured their cones in September-October, the majority did not mature their cones until middle or late December or even in January.

Accordingly, the second trip was made late in December 1955. Both authors plus Mr. Chester Rowell, taxonomist from the Biology Department of the Texas A & M College and Mr. Rocha went on the second trip. The cone crop was plentiful on most species and abundant collections were possible.

The area from which most of the collections were made is in the extreme southern end of Nuevo León (fig. 1). As one goes into the mountains from Linares, the road which follows the stream bed rises sharply, going through the village of Itúrbide and then breaking out onto a plateau near Galeana. This unimproved road then proceeds in a southerly direction down the "plateau" through the towns of Ascensión, Aramberri, and (in 1954) to Zaragoza. From Zaragoza a trail leads up the mountain to the village of La Encantada, at an elevation of about 10,000 feet (fig. 2). Collections were made along this entire route wherever pines occurred,

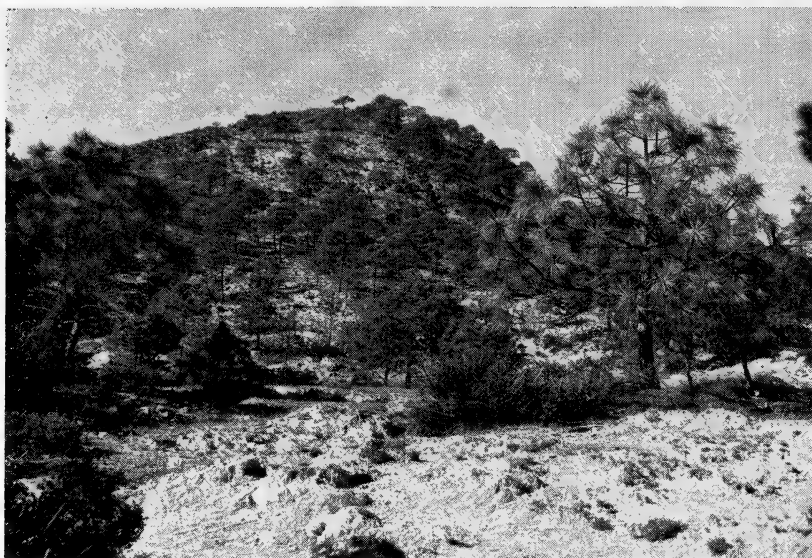


FIG. 3. *Pinus arizonica* var. *stormiae* on nearly solid rock in a very dry area near Ascensión.

most, however, being made up the mountain from Zaragoza and around La Encantada.

The collecting area described above varied from nearly desert near Galeana, Itúrbide, and Ascensión (fig. 3), with less than 20 inches rainfall, to the well-watered mountain forests around La Encantada. The higher elevation collections around La Encantada were in virgin forests, which included conifers of the genera *Abies* (fig. 2) *Pseudotsuga*, and *Taxus*. This is a most beautiful region, lush with vegetation. It is very similar in character to the middle-high elevations on the west side of the Sierra Nevada of California. Access is difficult, due to the poor roads and the necessity for horseback travel over considerable distances. This limited the specimens that could be collected. As far as could be determined, the pines around La Encantada had not previously been collected and classified, though Martínez (1948) mentions pine specimens from the area near Zaragoza.

Small collections were made from two other areas, one on Chipinque near the city of Monterrey, and the other in the Sierra Picachos near the village of Sombreretillo. This latter area is several miles to the east of the point where the Inter-American Highway from Laredo to Monterrey crosses the small range of mountains south of Sabinas Hidalgo.

All timbered regions at the lower elevations have been severely depleted. A crude method of bleeding for gum (oleoresin) is used extensively in the lowland areas, and in many cases so intensively and carelessly as to kill the trees (fig. 4). Fires and over-grazing have taken a huge toll and in



FIG. 4. Method of bleeding tree for gum (oleoresin). Note "cup" chopped in tree at base of peeled face.

many of the very scattered older stands, reproduction is lacking. There are indications in some areas that previously pine-covered land may degenerate to desert scrub if present treatment continues. Conversely the high mountain, virgin forests contain considerable overmature timber that is dying out. This could well be harvested if there were any method whereby the timber could be economically transported to markets.

In 1955, twenty-eight separate pine collections were made from the three areas visited. Each included: 1) ripe cones, up to a bushel from a single tree (these "green" cones were brought to Texas and the seed was extracted there); 2) a specimen fruiting branch, which contained mature cones, yearling cones, undamaged terminal bud, and typical foliage. These fruiting branches were pressed in the field; before this was done, however, a detailed study was made of their needles, buds, and other features, and colored photographs were taken to record foliage color, needle length and number, color and shape of unopened cone, color, position, and number of yearling cones, bud color, fuzziness, etc. In addition, needle bundles were preserved in formaldehyde-acetic acid-alcohol solution; these were later sectioned for the study of needle anatomy and morphology.

Current literature (Loock, 1950; Martínez, 1945 and 1948; Dallimore and Jackson, 1948) proved inadequate to the task of identification owing to the many recent changes in Mexican pine taxonomy and to the fact that the collections showed much intergradation. In order to make satisfactory species identifications of our collections, it thus became necessary to make a thorough analysis of all characters, including cross-sections of the needles, and then refer back to original sources in the literature of the genus.

#### SEEDLING CHARACTERISTICS

In all books referred to, there is a notable absence of reference to seedling characters. Such characters are of importance, especially since many of the Mexican species show a tendency to have delayed height growth, i.e., a semi-grass stage of development. This tendency towards a grass stage of development might well be a key diagnostic feature, as is true for the intensively studied "southern pines" in the longleaf-loblolly-slash pine complex. A tree with a true grass stage grows one to many years putting on only very little height growth, the needles being borne near the ground and appearing as a clump of "grass." A tree with a semi-grass stage makes only very little height growth the first year, but some stem is evident; in subsequent years it may, or may not, put on rapid height growth. The seedlings of the material collected varied from nearly a true grass stage to normal height growth (fig. 5).

Seedlings of all collections in this study have gone through one growing season in the nursery. Their characters will be discussed in the species list which follows.

#### PINUS SPECIES COLLECTED IN NUEVO LEÓN

Many species of pines, and their intergrades, were found in Nuevo León, with several species commonly growing completely intermixed.

Mexican pines do not display some of the usual differences held to be diagnostic of hard- or yellow-pines as contrasted with the soft- or white-pines. For example, many of the Mexican hard-pines contain five to seven or even more needles per fascicle, and five needles might be considered to be the rule rather than the exception. Conversely, the only true white-pine collected on this trip (*Pinus ayacahuite* var. *brachyptera* Shaw) had



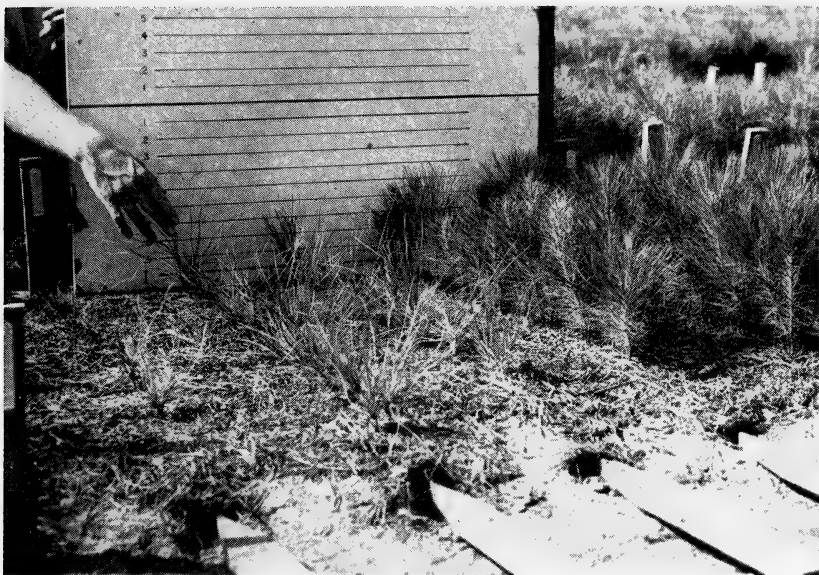


FIG. 5. Seedlings of *Pinus hartwegii* (on left) showing tendency toward a modified grass stage; seedlings of *P. teocote* (on right) showing normal growth in height and a basal crook in stem similar to shortleaf pine (*P. echinata*).

many fascicles containing only three needles instead of the normally expected five.

The five-needle hard-pines were most difficult to classify. Especially so were six specimens that exhibited characters of *P. montezumae* Lamb., *P. montezumae* var. *lindleyi* London, *P. pseudostrobus* var. *estevezi* Martínez, and *P. durangensis* forma *quinquefoliata* Martínez. Their characters did not fit any taxon completely, and after careful study the conclusion was drawn that they were intermediate or intergrading forms. Such intermediacy might well be called the rule here, especially for the five-needled pines. Both Loock (1950) and Martínez (1948) call attention to the intergrading forms and the complexity of the classification.

Four trees were found that had characters sufficiently dissimilar to previously described species so that they could not be definitely classified. These are included at the end of the species list. Three of the pine species in the list which follows have not been previously reported growing in the state of Nuevo León (Loock, 1950, and Martínez, 1948).

In addition to the pines, collections were also made of the genera *Abies*, *Pseudotsuga* and *Taxus*. The authors at first thought that *Taxus* had acquired a new distribution record, until it was found that Hernández *et al.* (1951) reported *Taxus* in the neighboring state of Tamaulipas. Many different oaks (*Quercus*) were observed, as well as other hardwoods such as Madroño (*Arbutus*). This is an area rich in many forms of vegetation and an extended collection trip would be most worthwhile.

*PINUS AYACAHUITE* var. *BRACHYPTERA* Shaw. This species had intermediate characters, in many ways closely resembling *P. reflexa* Engelm. Needles were predominantly in fascicles of five, with many fascicles of 3, 4, and 6 being present on mature trees. Collections were made near La Encantada at an elevation of approximately 10,000 feet. This pine was growing among hard-pines, *Abies*, *Pseudotsuga*, and *Taxus*. The trees were very large on the better sites. Cones mature early (October and November) so no seeds were obtained.

*PINUS ARIZONICA* var. *STORMIAE* Martínez. Several collections of this species were made, from near Ascensión to the area around Galeana, at elevations from 5,000 to 6,000 feet. Classification was accurate. This species was growing on extremely rugged sites, with low rainfall. One collection was made on nearly pure calcareous soil, with little other vegetation being present. Seedlings, as well as mature trees, all had needles in fascicles of three. All seedlings had delayed height growth, a semi-grass stage of development.

*PINUS CEMBROIDES* Gord. Collections were made near Ascensión, at elevations around 5,000 feet; they were easily classified. This species was very widespread. Needles were mostly in fascicles of 2, a few fascicles having 3. Cones mature early and no seeds were collected.

*PINUS HARTWEGII* Lindl. Several collections were made of this species, most of which were easily classified. One collection had characters very similar to *P. rudis*. All collections were made near La Encantada, at elevations around 10,500 feet, in nearly pure stands. Needles were predominantly in fascicles of 5, some of 4. Seedlings all had their needles in fascicles of 3, and had a definite semi-grass stage (fig. 5). The seedlings looked somewhat like those of *P. pseudostrobus*, but were coarser.

*PINUS PSEUDOSTROBUS* Lindl. Two collections of this species were made, one fitting the classification well, the other having affinities with *P. hartwegii*. Collection was near La Encantada at elevations around 10,000 feet. These trees were growing in a mixed pine and fir stand, just below the pure *P. hartwegii*. Needles were mostly in fascicles of 5, with some of 6 and 7 present. Seedlings had needles in fascicles of 3, 4, and 5, and had a definite semi-grass stage similar to *P. hartwegii*.

*PINUS PSEUDOSTROBUS* var. *ESTEVEZI* Martínez. This species was collected only west of Iturbide at an elevation of 5,000 feet. It was fairly easily classified, though all characters did not exactly fit. It was growing under relatively droughty conditions. Needles were in fascicles of 5, with some 4 and 6. Seedlings had needles in fascicles of 5. Unlike *P. pseudostrobus*, height growth of the seedlings was normal.

*PINUS PSEUDOSTROBUS* forma *PROTUBERANS* Martínez. It was difficult to classify this species accurately since no foliage was collected. Cones were collected at dusk from three trees, all appearing to be the same until cones were closely examined. Two of the trees remain unclassified, having needle anatomy like *P. hartwegii*, foliage like *P. rudis*, and cones similar to *P. pseudostrobus* var. *estevezi*. The third tree had cones exactly like *P.*

*pseudostrobus* forma *protuberans*. Collection was made near Ascensión, at an elevation of 6,000 feet. Seedlings had a semi-grass stage, with needles in fascicles of 3, 4, and 5. This species has never been reported in Nuevo León, only from the more southern states.

PINUS MONTEZUMAE Lamb. Several collections were made of this species, and classification was from very exact to doubtful. Two collections were very similar to *P. montezumae lindleyi* and also to *P. pseudostrobus*. Specimens were obtained near Zaragoza, Escondida, Ascensión, Itúrbide, and in the Sierra Picachos near Sombreretillo, ranging in elevation from 3,500 to 6,000 feet. Needles were in fascicles of 5, with an occasional 4. The needles of seedlings were in fascicles of 3, 4, and 5, the predominant number varying from tree to tree. Seedlings had extra long needles and had normal height growth (no grass stage). This was different from seedlings obtained from seed previously sent to us as *P. montezumae*, all of which had a pronounced grass stage.

PINUS MONTEZUMAE var. LINDLEYI Loudon. Classification of this species is only partially satisfactory, some characters not fitting too well. It was collected near Zaragoza at 5,000 feet elevation. Needles were in fascicles of 5, with some of 4. Seedlings had needles in fascicles of 5 and had normal height growth. This species has not previously been reported in Nuevo León, only from the states to the south, including Hidalgo, Vera Cruz, and Querétaro.

PINUS TEOCOTE Schl. and Cham. Of the several collections of this species, only one was in doubt, because of the needle anatomy. Collections were made near La Encantada, Ascensión, and at Chipinque, near Monterrey. Elevations ranged from 4,500 feet to 10,500 feet. Needles were short, always in fascicles of 3. Seedlings had all their needles in fascicles of 3, and had normal height growth (fig. 5). All had an unusual crook at the base of the stem, similar to that found in shortleaf pine (*P. echinata* Miller). Just as for *P. montezumae*, seed sent to us under the name of *P. teocote* had a grass stage, while none of our own collections showed this feature.

PINUS DURANGENSIS forma QUINQUEFOLIATA Martínez. Three collections were made of this species, none of which were classified with exactness. Characters were found similar to *P. pseudostrobus estevezi*, *P. montezumae* and *P. pseudostrobus*. This species has not previously been reported in Nuevo León, being found to the west in the states of Chihuahua and Durango. Our collections were made at La Encantada, Chipinque, and Sombreretillo. Needles were in fascicles of 5, with a few 4, and occasionally 6. Seedlings from two of the trees had needles in fascicles of 5, while one (from Sombreretillo) had them of 3, 4, and 5. Seedlings were tall (no grass stage), with long needles.

PINUS RUDIS Endl. One poorly classified collection was made of this species, the tree having characters like *P. montezumae lindleyi* and *P. pseudostrobus*. Collection was made at La Encantada, at 9,500 feet elevation. Needles were in fascicles of five. Seedlings were tall and had needles in fascicles of three, four, and five.

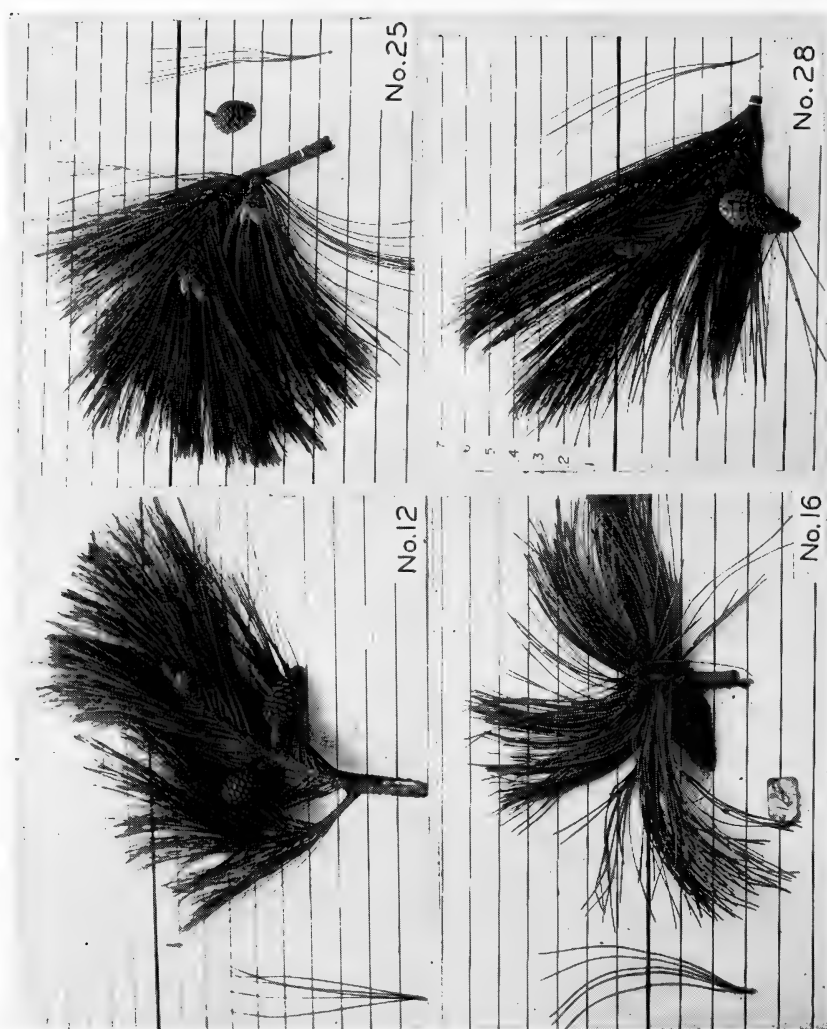


FIG. 6. Cones and foliage of unclassified trees, numbers 12, 16, 25, 28. Background board in 0.1 foot units.

The following *Pinus* collections from Nuevo León remain unclassified:

TREE No. 12 (fig. 6). Growing on a very dry site near Ascensión, with cacti and a few xerophytic shrubs. Surprisingly vigorous for a tree growing on such a poor site. Foliage with needles all in fascicles of five, about 20 cm. long, thin, flexible, slightly drooping; resin ducts two to four; endodermal outer wall thickened; hypodermis with moderate intrusions into chlorenchyma; two vascular bundles touching but distinct. Cone 8 cm. long; peduncle about 2 cm. long; color greenish black when unopened, changing to dark brown with drying; apophysis strongly keeled, somewhat reflexed on dorsal part of cone; umbo very small, prickle not sharp, not deciduous. Seedling with needles in fives, thin; having normal height growth.

TREE No. 16 (fig. 6). Collected only in one small valley above Zaragoza, growing intermixed with oaks at 6,000 feet elevation. Given by us the name "blue pine" due to the very bluish color of the foliage. Appearing to belong to the *P. rudis*-*P. hartwegii* complex, with intermediate characters. Foliage with needles predominantly in fives, about 18 cm. long, very stiff, twisted, glaucous blue-green; resin ducts seven to ten, medial; endodermal walls thin; hypodermis intruding slightly into chlorenchyma; two vascular bundles separated by several cell thicknesses of transfusion tissue. Cone about 10 cm. long, purplish black when unopened, olive brown when dried, asymmetric; apophysis flat to somewhat raised; umbo grey, sunken, very small. Seedling with needles in bundles of three, coarse; with modified grass stage.

TREE No. 25 (fig. 6). Growing in creek bottom, very rocky, Sierra Picachos, near Sombreretillo. Foliage with needles in threes, fours, and fives, predominantly fives, about 23 cm. long, moderately heavy, drooping, blue-green; resin ducts three to six, medial; endodermal outer walls thickened; two vascular bundles close together, not distinct; hypodermis very thick with small intrusions. Cone (old, hanging on tree; no fresh cones) about 5 cm. long; peduncle about 1.5 cm. long; apophysis raised with flat face, slightly keeled; umbo flat to sunken. Seedling none.

TREE No. 28 (fig. 6). From Sierra Picachos, near Sombreretillo. Needle number distinguishing this tree from *P. durangensis* and similar species. Foliage with needles predominantly in threes, few fours and fives, around 25 cm. long, somewhat pendent, moderately thin; resin ducts three and four, medial and one internal; endodermal outer walls variable, thick to slightly thick; two vascular bundles touching but distinct; hypodermis thick, with considerable intrusions. Cone about 9 cm. long, black to purplish green unopened, drying to light olive brown, somewhat asymmetrical; apophysis on dorsal side considerably reflexed, strongly keeled; umbo raised, ashy gray, with recurved, short, stout prickle. Seedling with needles in threes and fours, occasionally fives, thick; with normal height growth.

## ACKNOWLEDGEMENTS

The authors wish to thank all those who made these trips to Mexico possible and profitable. Dr. E. A. Pequeño is to be especially recognized for suggesting the trips, for accompanying the authors on both trips, and for helping to defray expenses incurred while in Mexico. He is to be commended for his interest in the natural resources of Mexico. We hope his conservation efforts will be successful.

Mr. Erasmo Cerda of Aramberri hosted both collection parties, and supplied housing, food, horses and guides necessary for the trip to La Encantada.

Mr. Chester Rowell helped considerably on the second trip with his knowledge of both the Mexican flora and language, as well as helping greatly on the photography.

The Medellín brothers acted as guides from Zaragoza, and welcomed the parties to La Encantada. Their help and friendliness certainly aided in making the North American visitors feel welcome in Mexico.

The several others that went as helpers or students on the trips were indeed appreciated. Everyone present contributed something to help enrich the value of the collections.

School of Forestry, Forest Genetics,  
North Carolina State College, Raleigh  
and  
Forest Genetics Laboratory, Texas Forest Service,  
College Station, Texas

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# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 5

JANUARY, 1958

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PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

# MADRÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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## PINUS OAXACANA, A NEW SPECIES FROM MEXICO

N. T. MIROV

In Oaxaca and adjacent states of Mexico is found a pine with very long, prominent projections of the apophyses of the cone scales. Though previously identified as a variety of *Pinus pseudostrobus* Lindl., this pine differs from *P. pseudostrobus* especially in the cones and in the chemical composition of the turpentine, and it is here published as a new species.<sup>1</sup>

**Pinus oaxacana** Mirov, sp. nov. *P. pseudostrobus* var. *apulcensis* Shaw pro parte, as to two specimens cited, not as to type, Pines of Mexico, p. 19, 1909. Non *P. apulcensis* Lindley, Edwards' Bot. Reg. 25, Misc. 63, 1839. *P. pseudostrobus* var. *oaxacana* Martínez as to description, not as to type, Las Pinaceas Mexicanas 1:195. 1945. Oaxaca pine. *Pinus* subgenus *Diploxylon* Koehne. Arbor 20–30 m. alta, ramulis vernis uninodalibus, glaucis; folia 5 in fasciculo, 20–33 cm. longa, serrulata, tenuissima, flexilia, pendula; stomata dorsalia pleurumque 5–7 seriebus et stomata ventralia 3–5 seriebus untrinque; hypodermis 2–4 seriebus cellularum, uniformis vel multiformis; ducti resinosi mediani, 2–4; endodermis cum septis exterioribus cellularum crassis; fasciculi vasculares 2, approximati; vaginae ca. 28–18 mm. longae, persistentes; strobili subterminales, 1–3, subsessiles, 10–14 cm. longi, clausi ca. 6 cm. lati, aperti ca. 9–11 cm. lati, ovoidei vel conici, acuti, leviter asymmetricales vel obliqui, ad maturationem aperientes, decidui super squamas infimas; apophyses ca. 12–20 mm. latae et ca. 8–12 mm. altae, rhomboideae, crassae, carinatae, cum projectione prominenti elongata 5–22 mm. longa, basi 5–12 mm. lata et 3–8 mm. crassa, pyramidalis vel conica, dura, complanata, recta vel curvata et reflexa; umbo in parte exteriori projectionis in puncto brevi terminens; projectiones inaequales, ad latum abaxialem strobili longiores; semen 6–7 mm. longum, obovoideum, atro-brunneum, cum ala separabili brunnea ca. 20 mm. longa et 8–9 mm. lata.

Resina terebintha n-heptane, 21 per centum; dextro- et dextro, laevo- $\alpha$ -pinene, 51 per centum; laevo- et dextro, laevo-limonene, 15–16 per centum; n-undecane, 1.3 per centum; et sesquiterpene, longifolene, 7.5 per centum componitur.

Tree 20–30 m. tall, the spring shoots uninodal, glaucous; leaves 5 in a fascicle, 20–33 cm. long, serrulate, very slender, flexible, drooping; dorsal stomata mostly 5–7 rows and ventral stomata 3–5 rows on each side; hypodermis of 2–4 layers of cells, uniform or multiform; resin ducts medial, 2–4; endodermis with outer cell walls thick; vascular bundles 2, close together; sheaths about 28–18 mm. long, persistent; cones subterminal, 1–3, subsessile, 10–14 cm. long, ovoid or conic, acute, slightly asymmetrical or oblique, opening at maturity, deciduous above lowest scales; scales

<sup>1</sup> Dr. Elbert L. Little, Jr., of the United States Forest Service, assisted in preparing the Latin and English descriptions and in checking the nomenclature.

with apophyses ca. 12–20 mm. broad and 8–12 mm. high, rhomboidal, thick, keeled, the apophyses with projections prominent, elongate, unequal (those on abaxial side of cone longer), 5–22 mm. long, 5–12 mm. wide at base, 3–8 mm. thick at base, pyramidal to conic, hard, flattened, straight or curved and reflexed, the umbo on outer part of each projection ending in a short point; seeds 6–7 mm. long, obovoid, dark brown, with detachable brown wing ca. 20 mm. long and 8–9 mm. wide.

The turpentine is composed of n-heptane, 21 percent; d, dl- $\alpha$ -pinene, 51 percent; l, dl-limonene, 15–16 percent; n-undecane, 1.3 percent; and a sesquiterpene, longifolene, 7.5 percent.<sup>2</sup> A herbarium specimen which serves as a voucher for the turpented trees was collected near Rancho Nuevo, 65 kilometers southwest of San Cristobal de Las Casas, Chiapas, Mexico (Mirov, in 1951) and is deposited at the Institute of Forest Genetics, Placerville, California.

Holotype. Near La Parada, Oaxaca, Mexico, altitude 7,500–9,000 feet, August 18, 1894, *E. W. Nelson 985* (US 398558). A slightly reduced drawing of the cone of the holotype which is about 13 cm. long, was reproduced by Shaw (1909, pl. 12, fig. 8; 1914; pl. 24, fig. 214). Another cone illustrated by Shaw (1909) is: *E. W. Nelson 2539* (US 398583), Miahuatlán, Oaxaca.

Under the name *P. pseudostrobus* var. *oaxacana* Martínez, detailed descriptions and good illustrations of *P. oxacana* were published by Martínez (1945, pp. 195–201; 1948, pp. 202–9) and by Loock (1951, pp. 161–164). In addition, both of these writers recorded it as occurring in the states of Oaxaca, Mexico, Puebla, Guerrero, Veracruz, and Chiapas.

In his treatment of the pines of Mexico, Shaw (1909) included this taxon as a variety of *P. pseudostrobus* Lindley (Edwards' Bot. Reg. 25, Misc. 63, 1839), basing his concept on Lindley's *P. apulcensis* (ibid.) and characterizing it as having "a greater or less prolongation of the apophyses." Shaw cited and illustrated three specimens: *E. W. Nelson 985*, La Parada, Oaxaca; *E. W. Nelson 2539*, Miahuatlán, Oaxaca; and *Pringle 8788*, Eslava, Distrito Federal. He assumed that all these specimens, as well as a cone collected by Hahn in 1866 at Cofre de Perote, Veracruz, and in the Museum d'Histoire Naturelle in Paris, were the same as *P. apulcensis* Lindl. from Apulco, Hidalgo.

Martínez (1945, pp. 168–201; 1948, pp. 184–209) recognized within *P. pseudostrobus* six variations (the typical variety, four named varieties and one form), differing chiefly in cone scale characters. Two of these named varieties and the form are pertinent herein. He showed clearly that the two Nelson Oaxaca collections, cited by Shaw as *P. pseudostrobus* var. *apulcensis*, belong to another taxon which he (Martínez) illustrated and described (in Spanish, loc. cit.) as *P. pseudostrobus* var. *oaxacana*. Unfortunately, Martínez failed to cite a type specimen, to publish a Latin

<sup>2</sup> This information was obtained from one sample, in which oleoresin from 25 trees was combined. In other samples the percentages may be different. Of significance is the presence of large quantities of a paraffin hydrocarbon, normal heptane.

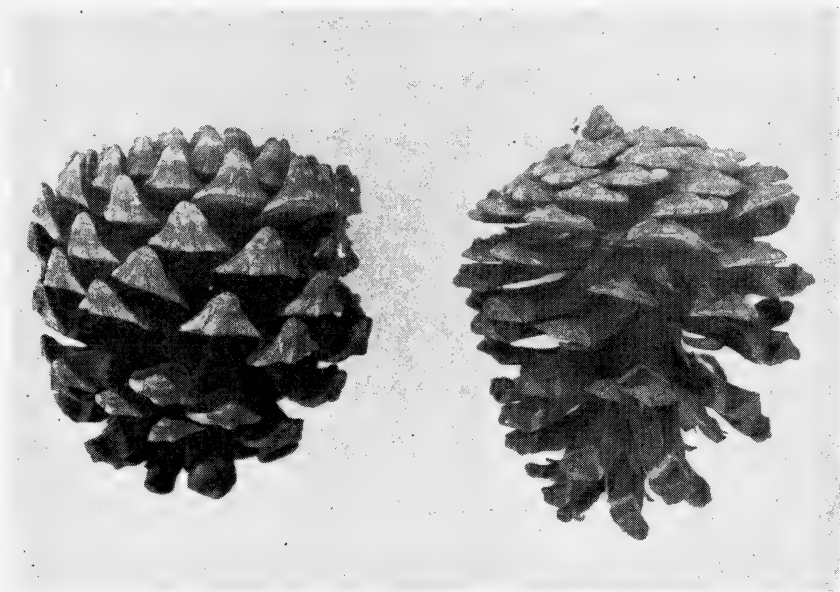


FIG. 1. Cone of *P. pseudostrobus* (left) ; cone of *P. oaxacana* (right). Both ca.  $\times \frac{1}{2}$ . Photo courtesy California Forest and Range Experiment Station, U. S. Forest Service.

diagnosis, or to designate the synonym *P. pseudostrobus* var. *apulcensis* (Lindl.) Shaw as applicable to his material only "in part." Therefore, although his intent was clearly otherwise, the name *P. pseudostrobus* var. *oaxacana* of Martínez must be referred to the type specimen (Hartweg in 1838, Apulco, Hidalgo) upon which both *P. apulcensis* Lindl. and *P. pseudostrobus* var. *apulcensis* (Lindl.) Shaw are based. Hence, it has been necessary to present a formal description and typification of the taxon represented by the Nelson Oaxaca specimens. To the pine from Apulco (*P. apulcensis* Lindley), Martínez (1945, p. 192; 1948, p. 199) assigned the name *P. pseudostrobus* var. *apulcensis*, an epithet which was superfluous when published, inasmuch as Shaw had already published this combination in 1909.

Under *P. pseudostrobus* var. *apulcensis*, Shaw cited a third collection with least prominent apophysis, *Pringle 8788* from Eslava, Distrito Federal. This collection had been distributed as *P. pseudostrobus* but had the synonym *P. protuberans* Roetzl also on the printed label. *Pringle 8788* is therefore referred to *P. pseudostrobus* forma *protuberans* Martínez (1945, p. 184; 1948, p. 192), which was characterized by the protuberant apophysis ending in a sharp point and which was recorded from Eslava as well as other localities.

However, it becomes desirable to establish the identity of the century-old prior species *P. protuberans* Roetzl (Cat. Grain. Conif. Mex. 27, 1857) from 9,000–10,000 feet altitude near Contreras, Distrito Federal. Bene-

dict Roezl (1824–85), a Czech plant collector and horticulturist, in 1857 and 1858 published names of nearly one hundred new species of *Pinus*, mostly from the vicinity of Mexico City, in two commercial catalogs of Mexican conifers. The original descriptions of Roezl's species were republished and translated by other authors, of which the following may be cited for *P. protuberans*: German, condensed, by Otto (Hamburg. Gart. Blumenzeit. 13:408. 1857); English by Gordon and Glendinning (Pinetum 259. 1858); Latin by Schlechtendal (Linnaea 29:348. 1858); and the original French by Carrière (Traité Gén. Conif. Ed. 2, 522. 1867).

Actually, Roezl characterized the five members of his Section VIII of *Pinus* as having five long needles and very prominent apophyses and protuberances, characters which indicate close relationship with the *P. pseudostrobus* complex and with *P. oaxacana*. Besides *P. protuberans*, this section had three other new species, *P. angulata* Roezl, *P. exserta* Roezl, and *P. heteromorpha* Roezl, and also *P. rudis* Endl. (a misapplication of that name).

Gordon (Sup. Gord. Pinetum 70, 1862; Pinetum Ed. 2, 319, 1875) examined Roezl's specimens and accepted *P. protuberans* Roezl, giving the other species of Roezl's Sect. VIII as synonyms under *P. protuberans*. Carrière (*ibid.*) also accepted *P. protuberans* Roezl, quoted the original description, and published a longer description of Roezl's dry specimens and living young plants. He reduced two species to varieties [*P. protuberans angulata* and *P. protuberans exserta*], and retained *P. heteromorpha* Roezl as a species. Parlatores [in DC., Prodr. 16(2):401–402. 1868] reduced *P. protuberans* and *P. heteromorpha* to synonymy under *P. pseudostrobus* Lindl. and placed *P. angulata* and *P. exserta* under *P. montezumae* Lamb. In a summary of 82 new species of *Pinus* in Roezl's catalog of 1857, Shaw (1909, p. 3 and table) cited the above and other references, noted that many of Roezl's specimens had been lost, and concluded that there was not a single valid species among the six or seven pines represented.

The epithets *P. protuberans* Roezl and *P. pseudostrobus* forma *protuberans* apparently refer to the same entity. The cone scale of *P. protuberans* has a protuberance, while that of *P. oaxacana* has a longer, more prominent projection. Therefore, because of the morphological and geographical differences, this pine from Oaxaca is not referable to any of Roezl's species.

*Pinus oaxacana* differs from typical *P. pseudostrobus* by the prominent projections of the apophyses of the cone scales. In the general part of his Los Pinos Mexicanos (Martínez, 1948, p. 37), Martínez showed drawings of the cone scales of his variety *oaxacana* and of *P. coulteri* D. Don as examples of protuberant apophyses.

When I collected oleoresin of Oaxaca pine in 1951 in Chiapas, Mexico, I found typical *P. pseudostrobus* and *P. oaxacana* growing together and I was much impressed by the difference in the cones. The heavy cones of Oaxaca pine resembled the cones of Shaw's group *Macrocarpae* (1914) more than the cones of typical *P. pseudostrobus*.

Shaw's group *Macrocarpae* consists of *Pinus torreyana* Parry, *P. coulteri* D. Don and *P. sabiniana* Dougl. In my opinion *P. jeffreyi* Murr. also is closely related to this group since, among other considerations, it crosses naturally with *P. coulteri*. Besides the morphological and genetic affinities of these pines, they all have common biochemical characters. Their turpentines all contain aliphatic hydrocarbons, either normal heptane C<sub>7</sub>H<sub>16</sub> or normal undecane C<sub>11</sub>H<sub>24</sub> or both (Table 1).

Turpentine of *Pinus pseudostrobus* was analyzed by Iriarte (1946), and was found to contain over 90 percent of d- $\alpha$ -pinene and a small quantity of an unidentified sesquiterpene. Turpentine of *P. oaxacana* has an entirely different composition. It contains: n-heptane, 21 percent; d, dl- $\alpha$ -pinene, 51 percent; l, dl-limonene, 15-16 percent; n-undecane, 1.3 percent; and a sesquiterpene, longifolene, 7.5 percent (Iloff and Mirov, 1953). Chemically *P. oaxacana* has much more in common with the pines of the group *Macrocarpae*, including *P. jeffreyi*, than with *P. pseudostrobus* (Table 1).

TABLE 1. OCCURRENCE OF SOME CHEMICAL SUBSTANCES IN THE TURPENTINES OF SEVERAL PINES

	n-heptane	$\alpha$ -pinene	limonene	n-undecane	longifolene	aldehydes	$\beta$ -phellandrene
<i>P. jeffreyi</i>	+	....	....	....	....	+	....
<i>P. sabiniana</i>	+	....	....	....	....	+	....
<i>P. coulteri</i>	+	+	....	+	....	+	+
<i>P. torreyana</i>	+	....	+	+	+	+	....
<i>P. oaxacana</i>	+	+	+	+	+	....	....
<i>P. pseudostrobus</i>	....	+	....	....	?	....	....

The proposal to elevate Oaxaca pine to a specific rank is based on consideration of both morphological and biochemical characteristics of the pine. The use of biochemical characters for taxonomic purposes is gaining more and more ground among taxonomists, especially in view of the brilliant research on Australian trees by Penfold (1935) and his co-workers. Among the pines, *Pinus jeffreyi* is an outstanding example of the validity of biochemical characters in taxonomy. This pine has been considered by some botanists for a long time as a variety of *P. ponderosa* (Shaw, 1914). Lately, however (and at least, partly because of profound chemical differences of the two pines) *P. jeffreyi* has been reinstated to its original status as a valid species.

*Pinus oaxacana* apparently crosses naturally with *P. pseudostrobus*. It is entirely possible that great variability in the structure of the cone scales within the *P. pseudostrobus* complex has been caused by hybridization

between these two pines. *Pinus oaxacana* also probably crosses with some varieties of *P. montezumae*, but consideration of such behavior is beyond the scope of this paper.

Institute of Forest Genetics,  
California Forest and Range Experiment Station,  
U. S. Department of Agriculture, Forest Service,  
Berkeley, California.

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#### CHROMOSOME COUNTS IN SECTION ERYTHRANTHE OF THE GENUS MIMULUS (SCROPHULARIACEAE)<sup>1</sup>

ROBERT K. VICKERY, JR., BARID B. MUKHERJEE, AND DELBERT WIENS

Brozek (1932) of Charles University, Prague, has determined the chromosome numbers of three horticultural plants of *Mimulus cardinalis* to be  $2n = 16$ . These counts were made in connection with his investigation of the genetics of flower color in this species. The senior author also has carried on work on the inheritance of flower color in the *M. cardinalis* complex (Vickery and Olson, 1956). In addition he is undertaking a bio-systematic study of the group. These investigations have necessitated a survey of the chromosome numbers of both the horticultural populations and the cultures of the wild races being used in these two studies. Herbarium specimens of all the cultures counted are deposited in the Garrett Herbarium of the University of Utah under the culture numbers given in Table 1.

<sup>1</sup> The work was supported by grants from the National Science Foundation and the University of Utah Research Fund. The authors wish to thank Drs. W. W. Newby and C. M. Woolf for their helpful criticisms of the manuscript.



TABLE 1. CHROMOSOME COUNTS IN MIMULUS, SECTION ERYTHRANTHE

## A. CULTURES OF NATIVE SPECIES

n = 8 *M. lewisii* Pursh

Porcupine Flat, Mariposa County, California, altitude 8000 feet,  
Sept. 17, 1948, *Hiesey* (5032).

Above Alta, Salt Lake County, Utah, altitude 8700 feet, *Vickery* 207  
(5875).

n = 8 *M. verbenaceous* Greene

Narrows Trail, Zion National Park, Washington County, Utah,  
altitude 4400 feet, April, 1956, *Wiens* (5264).

Bright Angel Creek, near Phantom Ranch, Grand Canyon National  
Park, Coconino County, Arizona, altitude 2000 feet, Nov. 4, 1954,  
*Jackson* (5924).

n = 8 *M. cardinalis* Dougl.

Beaver Creek, Siskiyou County, California, altitude 1800 feet,  
*Hiesey* 555 (5031).

## B. CULTIVATED COLOR FORMS

n = 8 *M. cardinalis* Dougl.

5077 Royal Botanic Garden, Edinburgh, Scotland.

5078 Regional Park Botanic Garden, Berkeley, California.

5308 Botanic Garden, Halle, Germany.

5309 Botanic Garden, Basel, Switzerland.

5310 Botanic Garden, St. Gallen, Switzerland.

5311 University Botanic Garden, Liège, Belgium.

5312 Botanic Garden, Antwerp, Belgium.

5313 Botanic Garden, Wageningen, Netherlands.

5315 University Botanic Garden, Brno, Czechoslovakia.

5316 Botanic Garden, Cluj, Roumania.

5318 Botanic Garden, Copenhagen, Denmark.

Brozek made his counts from the tips of adventitious roots, fixing them in Navashin's fluid and staining them with either Heidenhain's iron haematoxylin or Cajal's magenta and picro-indio-carmine stain (Brozek, 1932). We obtained good results with the method previously described (Mukherjee, Wiens, and Vickery, 1957) which employs fixation of the buds in acetic or propionic acid followed by squashing and staining in either aceto-carmine or propio-carmine.

The sources of the horticultural color forms and of the wild cultures which we have studied are given in Table 1. The chromosome number appears to be  $n = 8$  in all cases (fig. 1) although the preparations of *M. verbenaceous* (5264) showed occasional cells with apparently 9 or 10 chromosomes instead of the usual 8. The chromosomes of the 5077 culture of *M. cardinalis* were noticeably larger than the average for other races of the species (fig. 1). Those of the 5875 culture of *M. lewisii* were appreciably smaller than those of any other culture of the complex which we have examined. These size differences in the chromosomes suggest that there may be structural differences which in turn may account for the barriers to hybridization which we have observed when crossing *M. cardinalis* and *M. lewisii* (Vickery, 1956). Initially, all crosses produce vigorous  $F_1$

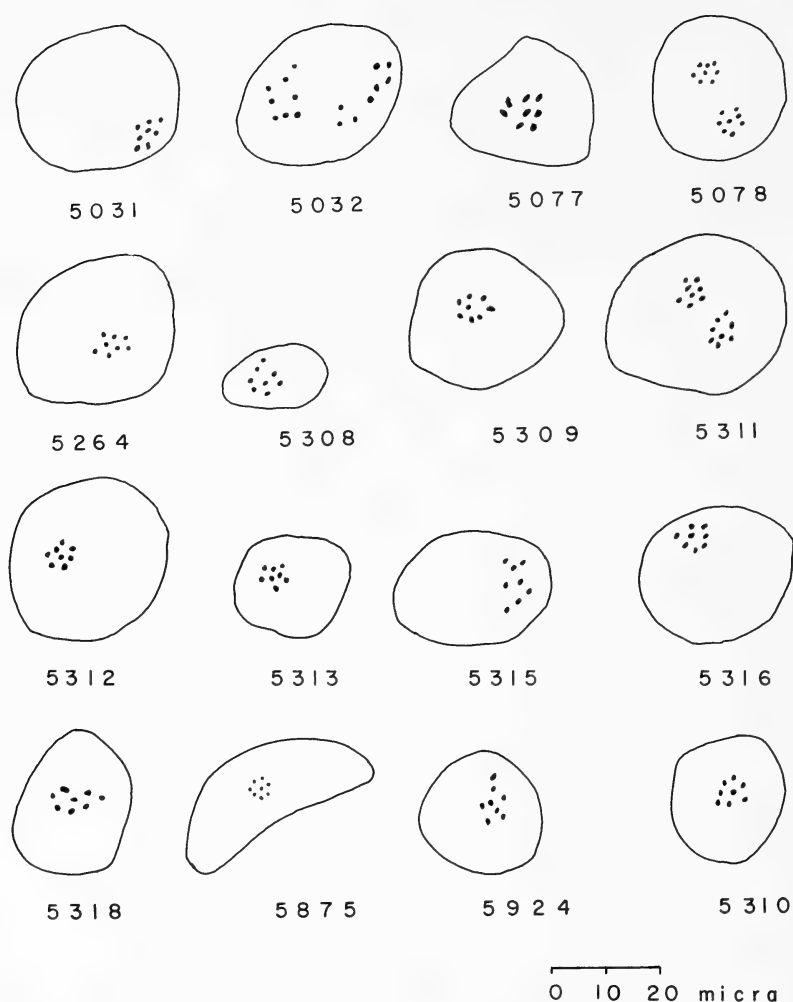


FIG. 1. Meiotic chromosomes of pollen mother cells of *Mimulus*,  $\times 750$ . Chromosome numbers of all the cultures are  $n = 8$ . Camera lucida drawings were made in all cases. The pollen mother cells of cultures 5077, 5264, 5308, 5309, 5318, and 5875 are in first metaphase whereas all the others are in second metaphase, but the two figures of the second metaphase were drawn only if the counts were clear in both nuclei.

populations but frequently the  $F_2$  and  $F_3$  generations are marked by decreased fertility. The crosses between *M. verbenaceus* and *M. cardinalis* and between *M. verbenaceus* and *M. lewisii* yield vigorous, fertile  $F_1$  hybrids, also.

Combinations of *M. cardinalis* or *M. lewisii* with species of section *Paradanthus* consistently failed (Vickery, 1956). *Mimulus moschatus*

Doug., *M. primuloides* Benth., and *M. bioletti* Eastw. were used to represent section *Paradanthus*. Six different reciprocal crosses were attempted using an average of five flowers each. A *Paradanthus* intrasectional combination of *M. moschatus* and *M. floribundus* Dougl. produced vigorous but sterile  $F_1$  hybrids. We have obtained only one chromosome count for this section: *M. moschatus*,  $n = 16$  (unpublished).

On the basis of these genetic and cytological results we believe that the most natural taxonomic treatment is to group the three taxa, *M. cardinalis*, *M. verbenaceous*, and *M. lewisii*, in section *Erythranthe*. This treatment follows that of Pennell (1951) rather than that of Grant (1924) where *M. lewisii* is placed in section *Paradanthus*.

Department of Genetics and Cytology  
University of Utah  
Salt Lake City 12, Utah.

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## TWO NEW SPECIES OF PENSTEMON IN COLORADO

C. WILLIAM T. PENLAND

Since the treatment of *Penstemon* for Harrington's "Manual of the Plants of Colorado" was prepared, additional collections and study have made it necessary to recognize the following two new species for the state.

***Penstemon harringtonii*** sp. nov. Herba perennis, glabra, 3- dm. 7 alta; caulibus erectis, simplicibus, glaucis; foliis glaucis, integris, crassis, obtusis vel acutis, mucronatis, basalibus spathulatis vel oblanceolatis, 5-7 cm. longis, 1.5-2.5 cm. latis, caulinis ceteris parvioribus, sessilibus, obovatis, elliptico-ovatis vel cordato-amplexicaulibus, ad inflorescentiam versus gradatim reductis; thyrsos cylindraco, angusto, interrupto, 5-10-fasciculato; calyce 5-9 mm. longo, lobis ovato-lanceolatis, acutis vel acuminate, scarioso-marginatis; corolla 18-24 mm. longa, coerulea (vel rosea), bilabiata, fauce ampliata; staminibus didynamis, inferioribus

corollae faucem multo excedentibus; antheris 2.5–3 mm. longis, glabris, sagittatis; loculis antherarum de apice ad basim dehiscentibus, confluentibus, haud explanatis; filamentum sterili dilatato (usque ad 1–1.5 mm. latitudine), pilis 1–2 mm. longis, dense aurato-barbato; capsulis ignotis.<sup>1</sup>

Glabrous perennial, 3–7 dm. tall; stems one to few, simple, erect, glaucous below, often purplish, especially above; leaves entire, thickish, glaucous, mucronate, the basal 1.5–2.5 cm. wide, 5–7 cm. long, spatulate to oblanceolate, obtuse to acute, the lower cauline 1–2 cm. wide, 2–5 cm. long, obovate, elliptic or ovate, acute, the upper cauline gradually reduced, ovate to cordate-clasping; inflorescence cylindrical, of 5–10 rather lax-flowered fascicles, one-third to one-half or more the height of stem; peduncles surpassing bracts, especially above; bracts all acute, scarious-margined, the lower broadly sessile-clasping, the upper reduced and inconspicuous, longer than wide; calyx 5–9 mm. long, the lobes ovate- to lance-acuminate, striate, narrowly scarious-margined; corolla 18–24 mm. long, pale to deep coerulean blue, often lilac-tinged on tube, or strongly pinkish-lilac throughout, the throat ampliate-funnelform, rather distinctly bilabiate, the lower lobes divergent but scarcely reflexed, the upper arched-erect; stamens conspicuously didynamous, the upper pair attached to corolla at its very base, the lower pair attached along corolla tube for about one-half their lengths, the free part then curved ventrally in the throat and well-exserted outward and upward to bring anthers opposite middle of orifice of corolla; anthers 2.5–3 mm. long, glabrous, sagittate, attached to filament at their middle or below, the connective wide, the sacs conjoined for one-half or more of their lengths, dehiscing throughout but not explanate, remaining parallel but curved; staminode glabrous to middle, then abruptly densely bearded with golden yellow hairs, those on the upper surface 1–2 mm. long, those on the lower surface prominent, but shorter and less dense, the staminode widened distally to 1–1.5 mm., rounded at tip and curved ventrally, usually a little exserted from orifice of corolla tube; mature capsules not seen.

Type. Abundant in sagebrush, altitude about 8000 feet, 3–5 miles northwest of Green Mountain Dam, Grand County, Colorado, 19 June 1952, *Penland 4296* (COCO; isotypes, COLO, CS, GH, NY, RM, UC, US).

Other known collections. COLORADO. Eagle County: rather dry slope 5 miles east of Wolcott, elevation 7200 feet, 7 June 1951, *H. D. Harrington 4935* (COCO, CS). Routt County: pinyon, cedar, sage association, elevation 7500 feet, 2 miles north of McCoy, Highway 131, 29 June 1951, *M. & C. Norton s.n.* (COCO, CS).

*Penstemon harringtonii* is readily recognized both in the field and in the herbarium by its two well-exserted stamens (fig. 1), a character that appears remarkably constant. Judged on the basis of its anthers it is most closely related to *P. cyathophorus* Rydberg, and it is therefore referred to the section *Coerulei* (as defined by Pennell, 1935). It differs

<sup>1</sup> The assistance of Mr. Robert M. Ormes in preparation of Latin diagnoses is gratefully acknowledged.

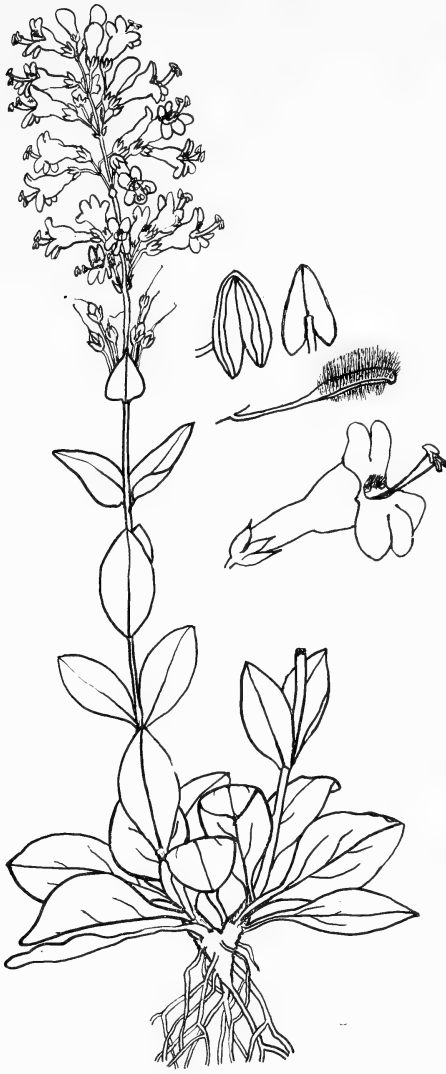


FIG. 1. *Penstemon harringtonii*. Habit, ca.  $\times \frac{1}{8}$ ; anthers,  $\times 5$ ; staminode, ca.  $\times 1\frac{1}{2}$ ; flower,  $\times 1$ .

from *P. cyathophorus* in its larger flowers (18–24 mm. long as compared to 9–15 mm.), in having only two instead of its four stamens strikingly exserted, in its longer anthers (2.5–3 mm. as compared with 2 mm.), and in its strongly reduced bracts, which are mostly longer than broad (the reverse is true of *P. cyathophorus*). In general appearance, however, *P. harringtonii* is more like *P. osterhoutii* Pennell (same section), to which it

was first referred, than it is like *P. cyathophorus*. Although the flowers average 14–20 mm. long in *P. osterhoutii*, thus approaching those of *P. harringtonii*, the anther sacs are widely divaricate and not at all sagittate as in *P. harringtonii*, and the stamens are not or scarcely exerted in *P. osterhoutii*. These closely related species may be keyed as follows:

Anthers sagittate with parallel sacs; 2 or all 4 stamens well-exserted.

Flowers 18–24 mm. long; only 2 stamens exerted; anthers 2.5–3 mm. long; bracts mostly longer than broad.....*P. harringtonii*

Flowers 9–15 mm. long; all 4 stamens exerted; anthers 2 mm. long; bracts mostly broader than long .....*P. cyathophorus*

Anthers with sacs divaricate; stamens not or scarcely exerted.....*P. osterhoutii*

The three cited collections of *P. harringtonii* represent a distribution of this plant on both sides of the Colorado River drainage system, and, to the south, on both sides of the Gore Range (Eagle and Blue rivers). The known range of *P. cyathophorus* (Grand and Jackson counties in Colorado, and in adjacent southern Wyoming) is to the north of that of *P. harringtonii* (Eagle, Grand, and Routt counties, Colorado), although at one place in Grand County the two species occur within 2–3 miles of each other. *Penstemon osterhoutii*, the other species closely related to *P. harringtonii*, is common to the west of *P. harringtonii* in Eagle and Garfield counties, but the ranges of the two do not overlap. Moreover, *P. harringtonii* occurs at elevations of 7200–8000 feet, while *P. osterhoutii* has not been collected above an elevation of 6600 feet.

The unusually interesting *Penstemon acaulis* Wms. was first collected in Sweetwater County of southwestern Wyoming. Later it was found in adjacent Daggett County in Utah. So far as is known it has not been reported from south of the Uinta Mountains in Utah, or from the northwestern corner of Colorado. In 1951 the writer collected a *Penstemon* which was at first presumed to be only a more robust form of *P. acaulis*. It was found a few miles east of Elk Springs, south of the Yampa River in Moffat County, Colorado, a locality approximately eighty airline miles southeast of the nearest known station for *P. acaulis*. In order to secure better diagnostic material this area was again visited in 1952 and 1953. In those years two additional stations for the plant were discovered; both of these were north of the Yampa River, between Greystone and the Little Snake River. The collections and all material observed in the field are quite uniform in aspect, and continued study has led to the proposal of the following new species, whose closest relative is clearly *P. acaulis*.

***Penstemon yampaensis* sp. nov.** Herba caespitosa perennis, 3 cm. vel minus alta; rhizomatibus ramosis; foliis 15–30 mm. longis, 2–4 (–5) mm. latis, oblanceolatis, acutis, cinereis, spiculato- vel papillato-pubescentibus, plus minusve viscidis; calyce 5–9 mm. longo, viscido-pubescente, lobis acuminatis, inferne scarioso-marginatis; floribus 2–4 in ramo terminali; corolla 15–18 mm. longa, pallide roseo-purpurea (vel demum coerulea), extus glanduloso-pubescente, basi faucis rotundatae haud pli-



FIG. 2. *Penstemon yampaensis* (Penland 4415). About  $\times 1$ .

catæ aliquantulo ventricosæ aureo-barbata, lobis posterioribus quam ceteris brevioribus; staminibus inclusis; loculis antherarum 1–1.5 mm. longis, glabris, confluentibus, haud late explanatis; filamentis sterilibus paulo exsertis, insuper aureo-barbatis; capsulis fere globosis, 4 mm. longis, glabris; seminibus 2–4, nigris, lunatis, rugosis.

Caespitose, essentially acaulescent perennial, spreading from branching rootstocks and in the open forming loose mats up to one foot in diameter, 3 cm. or less in height; leaves cineraceous, 15–25 (–30) mm. long, 2–4 (–5) mm. wide, oblanceolate, acute but not mucronate, scabro-pubescent with low, blunt, papilliform hairs (common on upper portion) or longer, straight or somewhat recurved, spiculate hairs (common toward base and petiole), the foliar hairs not gland-tipped but evidently viscid; mid-rib and two or more lateral veins prominent on dried specimens; flowers usually 4 (2–6) on each of the very short ultimate branches, often exceeded by the foliage; calyx 5–9 mm. long, the lobes long-acuminate, rather densely viscid-pubescent, narrowly scarious-margined below; corolla 15–18 mm. long, lilac, or with strong bluish tinge when older (?), on dried specimens usually blue, glandular-pubescent externally, golden- (to whitish-) bearded in throat below, the two upper lobes arched-erect, but little shorter than the less divergent three lower lobes (which may reach a length of 5 mm.), the throat moderately ampliate above short tube, some-

what ventricose, not at all plicate; stamens with longer pair reaching limb of corolla, the anther sacs 1–1.5 mm. long, ovate to oblong-ovate, glabrous, minutely denticulate along suture, divaricate, dehiscent confluent, not explanate; the staminode exerted from throat, bearded all along its dorsal surface with golden hairs, a little widened distally (to as much as 0.75 mm.), the apex emarginate; capsules nearly globose, about 4 mm. long, glabrous at maturity; seeds lunate, 2–3 mm. long, black, rugose and punctulate, 2–4 per capsule.

Type. Sandy, calcareous knoll, scattered grass and sage; 5.5–6 miles east of Elk Springs, Moffat County, Colorado, 9 June 1953, *Penland 4415* (COCO; isotypes, COLO, GH, NY, RM, UC, US). All other collections are from Moffat County, Colorado: type locality, 26 June 1951, *Penland 4236* (topotype, COCO); type locality, 20 June 1952, *Penland 4311* (topotypes, COCO, COLO, CS, GH, NY, RM, UC, US); 20 miles south of Vermillion Creek Bridge, 22 June 1952, *Penland 4326* (COCO, UC, US); 3–4 miles south of Greystone, 10 June 1953, *Penland 4426* (COCO, NY, RM).

A key serving to separate *P. acaulis* (fig. 3) and *P. yampaensis* (fig. 2) follows:

- Leaves essentially linear, 1–1.5 mm. wide, 10–20 mm. long; flowers 1 (–2) per ultimate floriferous shoot; corolla 14–16 mm. long, blue.....*P. acaulis*  
 Leaves oblanceolate, 2–4 (–5) mm. wide, 15–25 (–30) mm. long; flowers usually 4 (–6) per ultimate floriferous shoot; corolla 15–18 mm. long, lilac to bluish-lilac .....*P. yampaensis*

The foliar pubescence of these two species is essentially the same, though more of the spiculate hairs seem to be present in *P. yampaensis*, especially toward the leaf base. *Penstemon acaulis* was assigned to the section *Caespitosi* by Williams in his original description of this species (1934). Keck (1937) also assigned it to this group but changed the rank of the group to a subsection of the section *Ericopsis*. Keck pointed out, however, that in *P. acaulis*, "The character of its pubescence is unique in this group of species." There are two probable reasons for this uniqueness: 1) the papillate hairs, besides being short and blunt, are very broad at the base (commonly 44–73 microns, as compared to 14–25 microns for hairs of *P. caespitosus* Nutt., *P. crandallii* A. Nels., *P. retrorsus* Payson and *P. abietinus* Pennell, all of which Keck also places in the *Caespitosi*; 2) the external walls of these hairs in *P. acaulis* and *P. yampaensis* are smooth or nearly so, while those of the four species named just above are denticulate (as observed in boiled or cleared material, at 100 × magnification). In this connection it is of interest that the hairs of *P. moffatii* Eastw. (section *Aurator*) are also blunt and smooth-walled. Also, the apex of some leaves of *P. moffatii* may even show the papillate condition of *P. acaulis*, but the longer, blunt, recurved type of hair is typical for the species.

The midrib of leaves of dried specimens of both *P. acaulis* and *P. yampaensis* is prominent nearly throughout; in addition, *P. yampaensis* shows





FIG. 3. *Penstemon acaulis* (Penland 4419). About  $\times 1$ .

two or more prominent lateral veins. This type of veining is certainly rare in the *Caespitosi*. Although the midrib may be prominent, as in *P. crandallii*, this condition is found only in the petiolar portion of the leaf. In fact, I have found a leaf situation similar to *P. yampaensis* in only one other case, a specimen from the Uinta Mountains of Utah which I have doubtfully referred to *P. abietinus*. Two other collections of *P. abietinus* show leaves agreeing with the other *Caespitosi*. (I have not studied leaves of *P. thompsoniae* (Gray) Rydb., however.) The midrib of *P. yampaensis* is not only prominent but is also relatively large (sometimes over 400 microns in diameter in cleared material, as compared with under 200 microns in *P. caespitosus*). Probably correlated with the presence of large lateral veins in *P. yampaensis* is the fact that a number of leaves have been found showing 1-4 small teeth near the apex.

The non-plicate character of the corolla throat certainly poses a question as to the assignment of *P. acaulis* and *P. yampaensis* to the subsection *Caespitosi*, where their caespitose nature would apparently place them. In all the other six species of the subsection (Keck, *loc. cit.*), the 2-ridged and commonly laterally flattened, plicate throat is a constant and diagnostic feature. Nor do *P. acaulis* and *P. yampaensis* fit into the other two subsections of *Ericopsis* (*viz.*, the *Linarioides* and the *Laricifolii*). It seems to me that their affinity is rather with the section *Aurator*, through such species as *P. nanus* Keck, *P. dolius* Jones, *P. pumilus* Nutt., and *P.*

*moffatii* Eastw. Perhaps the least that can be said for them is that they help to emphasize more strongly the relation between the sections *Aurator* and *Ericopsis*, a point which was elucidated by Keck.

Colorado College,  
Colorado Springs, Colorado

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### PECULIARITIES OF THE COLUMBIA RIVER GORGE FLORA

LEROY E. DETLING

The gorge cut through the Cascade Range by the Columbia River as it flows westward between Washington and Oregon has long been recognized as a place of peculiar botanical interest. If one studies the distribution of the plant species found there, he is soon impressed by the large number that are either endemic to the area or occur as isolated populations significantly removed from their normal range. My interest in the history of the various elements of the Pacific Northwest flora led me to speculate upon the meaning of these peculiar distributional patterns. It seemed possible that an analysis of them might furnish clues to the rôle the Columbia Gorge has played in the migrations of vegetation in the past. Its physiography and geographical relationship to adjacent vegetation areas would in themselves lead one to believe that it might have served as a pathway for the migration of many types of organisms. With this in mind, I have spent considerable time during the past few summers studying the local distribution of those plant species occurring within the Gorge. This field work has subsequently been supplemented with herbarium studies on their wider distribution. The present paper is the result of this work.

The species listed herein by no means constitute a complete flora of the Columbia Gorge, although I have tried to make the lists as inclusive as possible. The collections of other botanists who have collected extensively here have also been studied, particularly those of Howell, Gorman, Henderson, Suksdorf, and Sheldon. Nevertheless, further search would undoubtedly reveal more species which might be included in the roster. However, I am confident that the list is sufficiently extensive to give us a good general picture of the significant features of the Gorge flora as a whole, its distribution in the various habitats, and its relation to outside populations, which was the chief purpose of this investigation. Any additions to the number of species will not increase the accuracy of a study made from this particular viewpoint.

## PHYSIOGRAPHY AND CLIMATE OF THE GORGE

The Cascade Range has been formed by a combination of gradual uplift since the Miocene epoch and of volcanic action largely during the Pliocene and Pleistocene. During this process the Columbia River, without materially altering its course, kept pace with the change by cutting its bed deeper and deeper, thus forming the great gash through the mountains which we know as the Columbia River Gap, or in a more restricted sense the Columbia River Gorge. Lateral erosion has been much slower than that carried on by the main stream, resulting in a deep canyon with precipitous walls, extending for some thirty-five miles. The small streams which flow into the river have cut their beds back into this canyon wall sometimes as much as a half mile, forming deep, narrow, lateral gorges into which the streams frequently plunge as waterfalls from a hundred to several hundred feet high.

Erosion has been less effective on the south wall of the canyon than on the north, and it is here that the most spectacular cliffs are to be seen. One of the most striking of these is the north face of St. Peter's Dome, which rises abruptly for about twenty-five hundred feet. Some of the cliffs have their bases almost at the river's edge, while others rise as much as a half mile or more back from the water. On the north wall of the Gorge the bases of the sheer drops are usually farther back from the river as well as higher up. A noticeable feature of both walls of the canyon is the frequent stair-step arrangement, apparently due to differences in hardness of the various strata of rock. It is of interest, but perhaps of no further consequence to us, that these steps, and therefore the shelves upon which much of the vegetation is growing, are roughly about six hundred feet one above the other. Thus there are a number of places where a shelf occurs about six hundred feet above the river, with other shelves above this at elevations of approximately twelve hundred and eighteen hundred feet. At most places the eighteen-hundred-foot shelf marks the top of the most abrupt cliffs, and the rise above that, while steep, is nevertheless a distinct slope, usually forested.

For an area so limited in extent the Columbia Gorge has an extremely varied climate. This is due in part to the depth of the canyon itself, in part to the influence of two entirely different climates at either end of the canyon, and in part to the general east-west orientation of the gap.

The curve of annual precipitation through the Gorge follows rather closely that of any transect extending from the Willamette Valley eastward across the Cascade Range to the central Oregon plateau. Although the level of the river bed rises comparatively little as one follows it eastward through the canyon, yet the elevation of the mountains that press in on either side is such as to raise the moisture-laden air masses from the Pacific Ocean sufficiently to cause a heavy precipitation over the central sector of the Gorge. The mean annual precipitation at Vancouver of 37 inches is typical for points along the lower Willamette and Columbia rivers. However, at Mount Pleasant, situated close to the western portal of

the Gorge, this figure has risen to 57 inches. Rainfall increases eastward to the vicinity of Cascade Locks where an average of approximately 75 inches is measured. Upstream from here there is a sharp drop in the annual mean. At Hood River and White Salmon about 30 inches are recorded, and at Lyle 25 inches.

Recorded data on temperatures in the Gorge do not tell us a great deal. Between Mount Pleasant and Hood River there is a gradual drop of  $4.7^{\circ}\text{F}$ . in the mean January temperature. In the same distance the mean July temperature rises  $2.3^{\circ}\text{F}$ .

One striking feature of the Gorge climate does not appear in the records. When atmospheric pressure differentials are favorable, masses of air move from eastern Oregon and Washington westward through the Gorge. In winter this situation frequently results in cold winds which at times reach very high velocities. When this occurs in conjunction with rainfall the result is often a very serious "silver thaw," i.e., a rain which freezes as it touches the ground, or trees and other vegetation. These freezing rains sometimes last for several days, and the breakage of trees and destruction of other types of plant life may be quite serious. A parallel situation frequently occurs during the summer when hot, dry east winds blow down through the gap, sometimes for several days at a time. The effect that such winds might have upon the vegetation is obvious.

As might be expected in a canyon with an east-west orientation, the local climate of the north wall is quite different from that of the south wall. This is clearly reflected in the difference in the general vegetation of the two sides. The flora of the dry, warm area of central Oregon and Washington extends much farther westward on the well-insolated south-facing slopes than on the north-facing wall, which is in deep shadow much of the time. On the other hand, the Douglas fir forest and its associates follow the cool north-facing slopes entirely through the Gorge to the Hood River Valley.

The significance of the Columbia Gap from the standpoint of such a climatic and vegetational barrier as the Cascade Range may be realized when we recall that it is the only point between the Fraser River in British Columbia and the Klamath River in northern California where the axis of the range has been cut through in such a way as to interrupt the continuity of all the life zones above the Transition. In this case the cutting has extended almost to sea level.

#### FLORA OF THE GORGE

To understand fully the flora of the Gorge and the implications of the distribution patterns of many of its species we must look first at the type of vegetation now existing in the adjacent lowlands at either end.

To the west the Gorge opens out upon what I have elsewhere called the Puget Area (Detling, 1948). This vegetation area occupies the broad valley between the Cascades and the Coast Range, extending from the south-

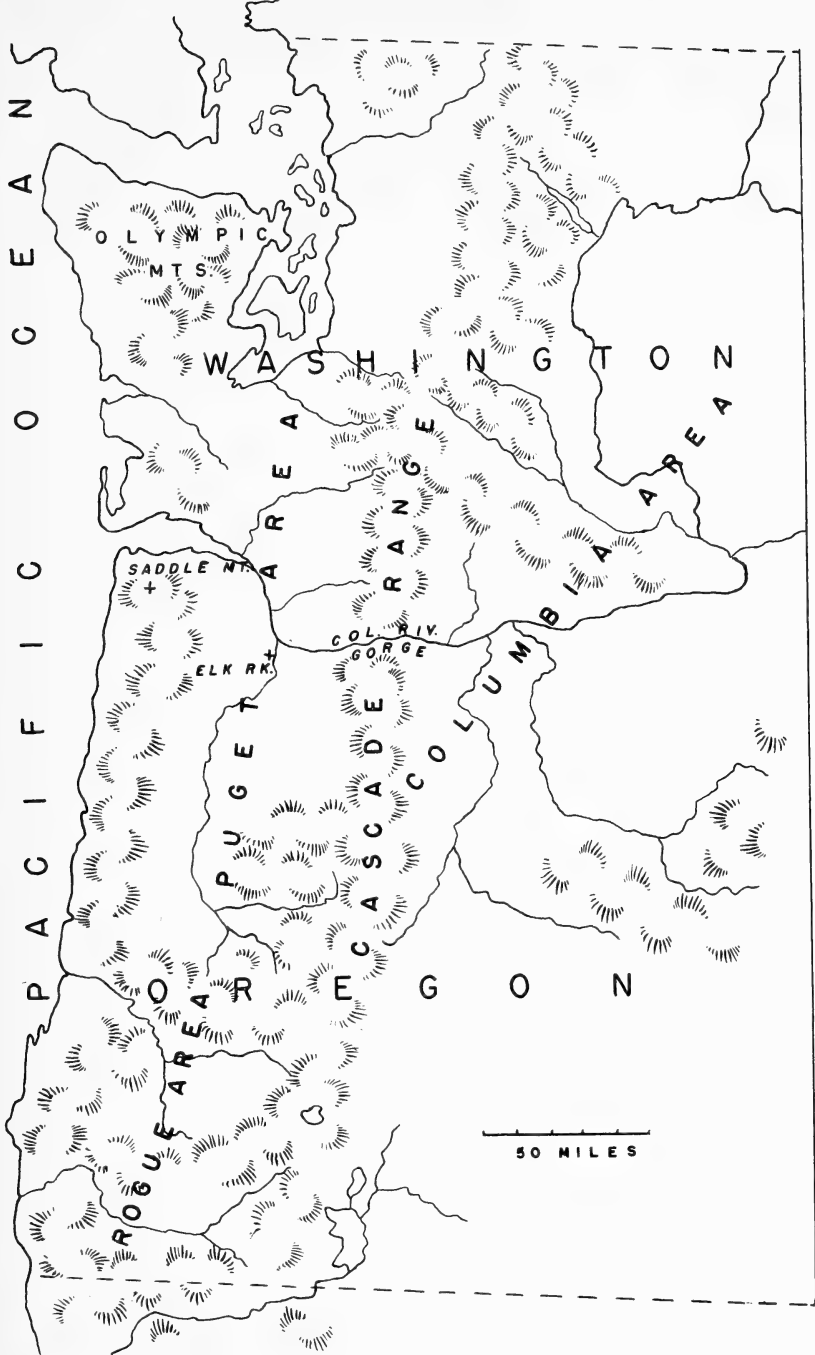


FIG. 1. Main geographic features of the Pacific Northwest related to the Columbia Gorge flora.

ern limits of the Willamette watershed in Oregon northward to Puget Sound and southern British Columbia. From a physiographic standpoint it coincides more or less with what the geomorphologists call the Puget Trough. The vegetation of the area is basically a Douglas fir forest, with an intermingling of oak-madrone woodland and grassland at lower levels and on the valley floor. Annual precipitation is high and neither summer nor winter temperatures are extreme. These conditions result in a dense forest cover, especially in the foothills, with an understory of vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), low Oregon grape (*Mahonia nervosa*), and red huckleberry (*Vaccinium parvifolium*), along with a wealth of herbaceous species.

Eastward the Gorge widens out and merges with the Columbia Area, again to use a name adopted by the author (op. cit.). This area occupies the valley of the Columbia River in north-central Oregon and south-central Washington, and such tributary valleys as those of the Yakima, John Day, and lower Deschutes rivers. The Hood River Valley comprises its westernmost extension. Annual precipitation is light throughout the area (13 inches at The Dalles). Winter temperatures are frequently very low, while the summers are hot. Apparently the region was originally a grassland, but there has been an invasion of sagebrush (*Artemisia* species) where the land has been overgrazed. Stands of ponderosa pine (*Pinus ponderosa*) are not uncommon on the hills where soil, moisture, and temperature conditions are favorable.

1. SPECIES OF WIDE DISTRIBUTION. For purposes of analysis I have found it convenient and useful to divide the Columbia Gorge species into groups according to their present general distribution. The first of these comprises a relatively large number of species (70, which is 34.0 per cent of the total of 206) which are widely distributed and occur at lower and middle elevations on both sides of the Cascade Range. From the standpoint of their origin this group can be divided again into two sub-groups—one whose members have probably come into our region from the north, the other evidently having originated to the south. In trying to determine where any given species has originated we may use several criteria. It is admitted that the use of any of these criteria alone would be unsound, but when they lend mutual support, and especially when applied to relatively recent migrations (from the standpoint of geological time), they probably present a fairly accurate idea of the direction of migration of most of the components of this flora. The criteria that seem most applicable to the problem at hand are: (a) The present maximum concentration of individuals of a species is likely to be somewhere near the area from which it has radiated in its migrations, and such concentration will probably be found in environmental conditions similar to those under which it originated. (b) A species is more likely to have come from a region where obviously close relatives are now located, than from a region in which such relatives are absent. (c) When a species typically occurs as a member of a definite species association, the area of origin of whose other

members can be postulated, we may assume it is safe to assign to it that same origin.

Judged on these bases the northern element of this first group consists of those species whose centers of distribution are to the north of the Columbia River; their present range frequently extends as far north as Alaska. At our latitude they are plants of shaded woodlands and stream banks, mostly associates of the coniferous forests. As might be expected from the dryness and high summer temperatures of the Columbia and Deschutes areas, the species tend to be absent from these two areas, but are common in the foothills and lower mountain slopes west of the Cascade crest and again in the Blue Mountains and in the Rocky Mountains of Idaho and Montana. It is highly probable that most of them migrated into our region by following the Cascade and Rocky Mountain ranges southward. The following species make up this sub-group:

<i>Adiantum pedatum</i> L.	<i>Mimulus guttatus</i> DC.
var. <i>aleuticum</i> Rupr.	<i>Physocarpus capitatus</i> (Pursh) Ktze.
<i>Aquilegia formosa</i> Fisch.	<i>Poa gracillima</i> Vasey
<i>Cerastium arvense</i> L.	<i>Poa nervosa</i> (Hook.) Vasey
<i>Chimaphila menziesii</i> (R.Br.) Spreng.	<i>Potentilla glandulosa</i> Lindl.
<i>Chimaphila umbellata</i> (L.) Nutt.	<i>Pseudotsuga menziesii</i> (Mirb.) Franco
var. <i>occidentalis</i> (Rydb.) Blake	<i>Pteridium aquilinum</i> (L.) Kuhn
<i>Circaea pacifica</i> Asch. & Mag.	var. <i>pubescens</i> Underw.
<i>Cirsium edule</i> Nutt.	<i>Rosa gymnocarpa</i> Nutt.
<i>Clintonia uniflora</i> (Schult.) Kunth.	<i>Rosa nutkana</i> Presl
<i>Cornus stolonifera</i> Michx.	<i>Rubus parviflorus</i> Nutt.
<i>Elymus glaucus</i> Buckl.	<i>Sambucus glauca</i> Nutt.
<i>Epilobium angustifolium</i> L.	<i>Sedum spathulifolium</i> Hook.
<i>Festuca occidentalis</i> Hook.	<i>Selaginella douglasii</i> (Hook. & Grev.)
<i>Festuca rubra</i> L.	Spring.
<i>Festuca subulata</i> Trin.	<i>Sisyrinchium idahoense</i> Bickn.
<i>Galium aparine</i> L.	<i>Smilacina racemosa</i> (L.) Desf.
<i>Geranium bicknellii</i> Britt.	<i>Smilacina sessilifolia</i> (Baker) Nutt.
<i>Heracleum lanatum</i> Michx.	<i>Symphoricarpos albus</i> (L.) Blake
<i>Heuchera micrantha</i> Dougl.	<i>Thalictrum occidentale</i> Gray
var. <i>pacifica</i> R.B.L.	<i>Thuja plicata</i> Donn.
<i>Linnaea borealis</i> L.	<i>Tiarella unifoliata</i> Hook.
var. <i>americana</i> (Forbes) Rehd.	<i>Trientalis latifolia</i> Hook.
<i>Lupinus polyphyllus</i> Lindl.	<i>Trillium ovatum</i> Pursh
<i>Lupinus rivularis</i> Dougl.	<i>Viola glabella</i> Nutt.
<i>Melica subulata</i> (Griseb.) Scribn.	

The species comprising the southern element of this first group have their present centers of distribution to the south of the Columbia River. None extends as far north as Alaska, although some reach southern British Columbia in the dry region east of the Cascades. West of the mountains they are most typically associated with the oak-madrone woodland, and when they occur at middle and higher elevations it is on exposed places with shallow soil, strong insolation, or other factors favoring a xeric flora. The members of this sub-group display less tendency to avoid the Columbia and Deschutes areas. They have probably arrived at our lati-

tude by way of the system of valleys west of the Cascades or by way of the valleys and plateaus adjacent to the Great Basin east of this range.

<i>Adenocaulon bicolor</i> Hook.	<i>Gilia capitata</i> Hook.
<i>Allium acuminatum</i> Hook.	<i>Holodiscus discolor</i> (Pursh) Maxim.
<i>Amelanchier florida</i> Lindl.	<i>Koeleria cristata</i> (L.) Pers.
<i>Apocynum pumilum</i> (Gray) Greene	<i>Lilium columbianum</i> Hans.
<i>Asarum caudatum</i> Lindl.	<i>Lotus douglasii</i> Greene
<i>Bromus vulgaris</i> (Hook.) Shear	<i>Madia gracilis</i> (Smith) Keck
<i>Castilleja hispida</i> Benth.	<i>Microsteris gracilis</i> (Dougl.) Greene
var. <i>hispida</i>	<i>Pinus ponderosa</i> Dougl.
<i>Crocidium multicaule</i> Hook.	<i>Prunus demissa</i> (Nutt.) Dietr.
<i>Cryptantha hendersonii</i> (Nels.) Piper	<i>Rhamnus purshiana</i> DC.
<i>Delphinium menziesii</i> DC.	<i>Sedum douglasii</i> Hook.
<i>Eriophyllum lanatum</i> (Pursh) Forbes	<i>Trifolium microcephalum</i> Pursh
<i>Erysimum capitatum</i> (Dougl.) Greene	<i>Zygadenus venenosus</i> Wats.

2. PUGET AREA ELEMENT. Another large group of species represented in the Gorge (54 in number and 26.2 per cent of the total) differs from the previously listed one in being restricted to the west side of the Cascade axis. They are, for the most part, common and widely distributed in the Puget Area and form a considerable part of its basic flora.

<i>Acer circinatum</i> Pursh	<i>Penstemon ovatus</i> Dougl.
<i>Acer macrophyllum</i> Pursh	<i>Penstemon serrulatus</i> Menz.
<i>Achlys triphylla</i> (Smith) DC.	<i>Phacelia nemoralis</i> Greene
<i>Alnus oregona</i> Nutt.	<i>Philadelphus lewisii</i> Pursh
<i>Anemone deltoidea</i> Hook.	var. <i>gordonianus</i> (Lindl.) Jeps.
<i>Arnica amplexicaulis</i> Nutt.	<i>Plectritis congesta</i> (Lindl.) DC.
<i>Aruncus silvester</i> Kostel.	<i>Polypodium vulgare</i> L.
var. <i>acuminatus</i> (Dougl.) Jepson	var. <i>occidentale</i> Hook.
<i>Asplenium trichomanes</i> L.	<i>Polystichum munitum</i> (Kaulf.) Presl
<i>Brodiaea coronaria</i> (Salisb.) Engler	<i>Prunus emarginata</i> (Dougl.) Walp.
<i>Campanula scouleri</i> Hook.	var. <i>mollis</i> (Dougl.) Brew.
<i>Cimicifuga elata</i> Nutt.	<i>Pyrola bracteata</i> Hook.
<i>Cornus nuttallii</i> Aud.	<i>Rhododendron macrophyllum</i> D. Don.
<i>Corydalis scouleri</i> Hook.	<i>Rhus diversiloba</i> T. & G.
<i>Corylus californica</i> (A. DC.) Rose	<i>Ribes bracteosum</i> Dougl.
<i>Delphinium oreganum</i> How.	<i>Ribes sanguineum</i> Pursh
<i>Dicentra formosa</i> (Andr.) DC.	<i>Romanzoffia suksdorfii</i> Greene
<i>Dryopteris arguta</i> (Kaulf.) Watt.	<i>Rubus spectabilis</i> Pursh
<i>Fragaria bracteata</i> Hel.	<i>Sambucus callicarpa</i> Greene
<i>Gaultheria shallon</i> Pursh	<i>Stachys emersonii</i> Piper
<i>Hydrophyllum tenuipes</i> Hel.	<i>Struthiopteris spicant</i> (L.) Weis.
<i>Iris tenax</i> Dougl.	<i>Tellima grandiflora</i> (Pursh) Dougl.
<i>Mahonia aquifolium</i> (Pursh) Nutt.	<i>Tiarella trifoliata</i> L.
<i>Mahonia nervosa</i> (Pursh) Nutt.	<i>Tolmiea menziesii</i> (Pursh) T. & G.
<i>Maianthemum bifolium</i> DC.	<i>Tsuga heterophylla</i> (Raf.) Sarg.
var. <i>kamtschaticum</i> (Gmel.) Jeps.	<i>Vaccinium parvifolium</i> Smith
<i>Melica harfordii</i> Boland.	<i>Valeriana sitchensis</i> Bong.
<i>Montia parvifolia</i> (Moc.) Greene	var. <i>scouleri</i> (Rydb.) Piper
<i>Oplopanax horridum</i> (Sm.) Miq.	<i>Vancouveria hexandra</i> (Hook.) Morr. &
<i>Oxalis oregana</i> Nutt.	Dcne.
<i>Oxalis trillifolia</i> Hook.	



3. COLUMBIA AREA ELEMENT. These species (27 in number, 13.2 per cent of the total) are typical members of the plant associations found in the Columbia Area, at least in its western portion, i.e., near the upper end of the Gorge. Some of them range beyond the confines of the area, occurring at relatively low elevations and in situations ecologically similar to those in the Columbia Area. When these occur west of the Cascades it is normally in the Rogue River Valley and southward, but not in the Puget Area.

\**Anemone oregana* Gray  
*Arnica cordifolia* Hook.  
*Bromus tectorum* L.  
*Castilleja hispida* Benth.  
     var. *acuta* Penn.  
 \**Crepis barbigera* Leib.  
*Dicentra cucullaria* (L.) Bernh.  
     var. *occidentalis* (Rydb.) Peck  
 \**Dodecatheon poeticum* Hend.  
*Eriogonum sphaerocephalum* Benth.  
     var. *tenue* (Small) Piper  
*Hackelia diffusa* (Lehm.) Johnst.  
*Helianthus cusickii* Gray  
 \**Hydrophyllum capitatum* Dougl.  
     var. *thompsonii* (Peck) Const.  
*Iliamna rivularis* (Dougl.) Greene  
*Lewisia rediviva* Pursh  
*Luina nardosmia* (Gray) Cronq.  
     var. *glabrata* (Piper) Cronq.

\**Lupinus leucopsis* Agardh  
     var. *bingensis* (Suks.) C. P. Sm.  
*Microseris nutans* (Geyer) Schultz-Bip.  
 \**Penstemon barrettiae* Gray  
*Penstemon richardsonii* Dougl.  
*Penstemon subserratus* Penn.  
*Philadelphus lewisii* Pursh  
     var. *lewisii*  
*Phlox speciosa* Pursh  
*Poa ampla* Merr.  
*Prunus emarginata* (Dougl.) Walp.  
     var. *emarginata*  
*Senecio integerrimus* Nutt.  
     var. *exaltatus* (Nutt.) Cronq.  
*Silene douglasii* Hook.  
*Spiraea lucida* Dougl.  
*Trifolium macrocephalum* (Pursh) Poir.

The six species preceded by an asterisk are of especial interest in that they occupy a very restricted region. They have their centers of distribution near the east end of the Gorge and are strictly endemic to this part of the Columbia Area. In the Gorge they usually occur toward the east end and, as might be expected, in fairly dry situations. Since the *Lupinus* and *Penstemon* species referred to here do not actually occur west of Mosier, it is doubtful whether they should be considered in our discussion of the Gorge flora. I list them merely because they form part of a flora which does have a definite relationship to the Gorge.

4. ROGUE AREA ELEMENT. A significant element of the Columbia Gorge flora (17 species, or 8.3 per cent) is typically associated with the oak-madrone woodland of the Rogue Area of southwestern Oregon (op. cit.), its components having their centers of distribution either there or farther to the south. However, they occur again rather frequently in the Columbia Area, especially in that portion near the upper end of the Gorge. These species rarely occur otherwise east of the Cascades. In the Puget Area they commonly appear as components of some rather striking islands of xeric vegetation growing on exposed rocky points in the Douglas fir belt (Detling, 1953). Their peculiar distribution pattern suggests the probability that during a warm, dry period they migrated northward from the

Rogue into the Puget Area, then eastward through the Columbia Gorge into the Columbia Area. During a succeeding cooler and moister phase of the climatic cycle these species have been much restricted in their occurrence in the Puget Area, and probably in the Gorge and in the Columbia Area as well.

Balsamorhiza deltoidea Nutt.	Leptotaenia dissecta Nutt.
Collinsia grandiflora Dougl.	Lotus micranthus Benth.
Collinsia parviflora Dougl.	Lupinus bicolor Lindl.
Comandra umbellata (L.) Nutt.	Lupinus laxiflorus Dougl.
Dichelostemma pulchellum (Salisb.) Hel.	Phacelia linearis (Pursh) Holz.
Eriogonum compositum Dougl.	Quercus garryana Dougl.
var. pilicaule St. J. & War.	Senecio harfordii Greenm.
Godetia amoena Lilja	Triteleia grandiflora Lindl.
Godetia quadrivulnera (Dougl.) Spach	var. howellii (Wats.) Hoover
	Viburnum ellipticum Hook.

5. BOREAL ELEMENT. A group of 31 species (15.1 per cent of the total) occurs normally at fairly high elevations in the Cascades, but is of interest here because its members are found rather abundantly at or near the bottom of the Gorge. Typically Canadian or Hudsonian Zone species, they usually range above 4000 feet. Some of them occur only in the Cascades, while others are found also in the mountain ranges both to the west and to the east of the Cascade axis; however, with only two or three exceptions they do not descend to the valley and plateau levels on either side. In the Gorge these species are nearly always found below the 1600-foot level, i.e., they are limited largely to the steep bluffs and cool lateral canyons, mostly on the south side of the river. In each case they are isolated from the main body of the population by a broad band of forested and less precipitous terrain in which I have so far found no record of their occurrence.

*Acer glabrum Torr. subsp. douglasii (Hook.) Wesml.	Menziesia ferruginea Hook. var. glabella (Gray) Peck
*Alnus sinuata (Regel) Rydb.	Mitella trifida Graham
*Antennaria racemosa Hook.	Penstemon nemorosus (Dougl.) Trautv.
Arabis furcata Wats.	Penstemon rupicola (Piper) How.
Arctostaphylos uva-ursi (L.) Spreng.	*Phlox diffusa Benth.
Arnica discoidea Benth. var. radiata (Gray) Cronq.	subsp. longistylis Wherry
*Campanula petiolata DC.	Polemonium carneum Gray
Cornus canadensis L.	*Polypodium vulgare L. var. columbianum Gilb.
Cryptogramma acrostichoides R. Br.	Populus tremuloides Michx.
Dodecatheon dentatum Hook.	*Saxifraga bronchialis L.
Dryopteris linnaeana C. Chr.	var. vespertina (Small) Rosend.
Habenaria unalaschensis (Spreng.) Wats.	*Saxifraga caespitosa L.
Haplopappus hallii Gray	Saxifraga rufidula (Small) Macoun
Lewisia columbiana (How.) Robins.	*Stenanthium occidentale Gray
*Lomatium angustatum (C. & R.) St. John	Suksdorfia violacea Gray
	Trautvetteria grandis Nutt.
	Vaccinium membranaceum Dougl.
	Woodsia scopulina D. C. Eaton

Ten species of the foregoing list (designated by asterisks) constitute an interesting group because of their relationship to the flora of Saddle Mountain. This peak is located in Clatsop County, Oregon, about 75 miles northwest of the western portal of the Gorge. Although only slightly over 3200 feet in elevation, it is the site of an isolated boreal flora which it may be assumed was at one time continuous with that now found in the Olympic Mountains (Detling, 1954). At the present time this flora has been eliminated from the areas between Saddle Mountain and the Olympics, and occurs only occasionally southward in the Oregon Coast Range, e.g., on Marys Peak. The ten indicated Columbia Gorge species have this peculiar and interesting distribution, occurring also on Saddle Mountain and in the Olympics, but so far as we know not between these points.

6. ENDEMIC SPECIES. Of the 206 species considered here as representing the flora of the Columbia Gorge, seven are endemic to the Gorge:

<i>Bolandra oregana</i> Wats.	<i>Erigeron oreganus</i> Gray
<i>Douglasia laevigata</i> Gray	<i>Hieracium longiberbe</i> How.
var. <i>laevigata</i>	<i>Sullivantia oregana</i> Wats.
<i>Erigeron howellii</i> Gray	<i>Synthyris stellata</i> Penn.

It is true that two of those included in this category, *Bolandra oregana* and *Sullivantia oregana*, have been found at one other station outside the Gorge, namely at Elk Rock on the lower Willamette River, and thus are not truly endemic to the Gorge and in the strictest sense of the term; however, they must be considered here in any discussion of endemism as it relates to the history of the flora.

Elk Rock is a sheer cliff on the west bank of the Willamette River a few miles above Portland and twenty-two miles by air from the west portal of the Gorge at Crown Point. The face of the bluff has an easterly and slightly northerly exposure; in certain spots seepage water keeps the surface wet most of the time. Apparently conditions here are sufficiently similar to those in certain niches of the Gorge to have encouraged the persistence of a few rare plant species which are otherwise found only in the cool, misty vicinity of the waterfalls of the Gorge. This situation suggests that during some period of glaciation in the Northwest the cold was intense enough to cause the extension of the boreal flora from the Cascades out over the valley floor at least as far as the Willamette River.

There are two possibilities always to be considered regarding the origin of narrowly endemic species. In the first place, they may be of relatively recent origin, having risen through mutation or hybridization from some pre-existing species in the area they now occupy. Theoretically, given time and proper environmental conditions, such a species would be expected to increase in number of individuals and to extend into nearby territory. On the other hand, endemic populations may be relicts of species which once were more widely distributed, but which, due to some factor such as failure to cope with a changing environment have been reduced to their present limited range.

Viewed as a whole, the endemic species of the Gorge would seem to be of the latter type. This conclusion is based upon the occurrence of two of them isolated at Elk Rock, upon the fact that they seem to be morphologically stable and not undergoing further evolutionary development, and finally that for the most part they have no near relatives in the vicinity.

These seven species are well-defined entities, and the plant taxonomist has no difficulty in placing them in the category of "endemics." However, when one studies carefully the wide-ranging species represented in the Columbia Gorge his attention is soon called to the fact that evolutionary processes have frequently taken place in the Gorge, and presumably are still going on, which have made that portion of the species slightly, but still noticeably, different morphologically from the rest of the population. Specialists in certain groups have already called attention to some of these, e.g., Cronquist (1955) for *Arnica amplexicaulis* and *Haplopappus hallii*, but they are frequently loath to give such local forms taxonomic standing. However, we cannot ignore the fact that they are there, and if we wished to follow the lead of less conservative botanists and give varietal or subspecific names to these local entities we could increase considerably the number of endemics in our list. These would of course be of the first type as to origin.

#### GENERAL DISCUSSION

Viewed from the standpoint of the major migrations of the Pacific Northwest flora, there are two outstanding phases in which the geographical situation, physiographic features, and structure of the vegetation of the Columbia River Gorge are probably significant.

The first of these is the rôle of the Gorge as a gateway for the passage of lowland species from one side of the Cascade axis to the other. For the rather large number of species (81, or 39.4 per cent) now confined to one side or the other of the axis, the Gorge obviously has not fulfilled this function. Even among the 70 species with a general distribution both east and west it is unlikely that many have migrated through the Gorge. Judging from their present widespread occurrence they probably reached the vicinity of the Gorge by paralleling the range on either side.

There is evidence, however, that a significant number of lowland species from other groups listed above have migrated through the Gorge in assuming their present distribution. Chief among these are the Rogue Area species found in the Columbia Area, with their isolated occurrences in xeric islands west of the Cascades. It was inferred in the earlier brief discussion of this group that the migration of its members through the Columbia Gorge took place from west to east. The basis for this inference is the fact that the centers of distribution of these species are to the south and west today, and any evidence of former occurrence is now found west of the Cascades. *Quercus garryana* may be cited as an example. This migration probably took place at a time of maximum northward extension of the Rogue flora. Floral migrations from an areal center normally occur

while climatic conditions at the center are becoming intensified and the environment in advance of the migration is becoming progressively more like that of the center. Since essentially the Rogue Area center is relatively warm and dry, the northward extension of the Rogue flora probably coincided with a xerothermic phase in the climatic cycle of the Pacific Northwest. Studies on post-glacial forest succession in the Northwest, based upon pollen profiles from peat bogs (Hansen, 1955), indicate that such a warm, dry phase did set in approximately 8000 years ago and lasted until about 4000 year ago, with its maximum probably about 6500 years from the present.

The other distinctive feature of the Gorge flora is the fact that such a large part of it constitutes an island of boreal forms isolated at the bottom of the main canyon or its smaller tributary canyons. These are in all probability relict occurrences, left from a time when the boreal flora, pushed to lower levels from above, was continuous from the middle mountain elevations down to the present valley level. It is hard to conceive that such a large number of species would have been established at their present levels by being transported from higher elevations across a transitional zone during a period of temperate climate. Rather, it is more likely that there was a general downward shifting of the flora during a cold phase of the climatic cycle, and subsequent isolation of many of the species in favorable niches as the climate became warmer and the main populations of the boreal species retreated to higher elevations. The presence of a number of Columbia Gorge species on Saddle Mountain and in the Olympics is another indication of a former continuity of the boreal flora at low levels in this part of the Pacific Northwest.

The narrow endemics briefly discussed above were probably reduced to their present restricted range during or following the culmination of this cold maximum. The occurrence of some of these isolated along the lower Willamette River may indicate that at one period their range at valley level was considerably more extensive.

The cold maximum which caused the downward migration of the boreal species must have preceded the warm, dry phase of climate previously mentioned, as the pollen profiles indicate only moderate cooling in the last 6000 years. These same profiles, correlated with radiocarbon datings (Broecker, Kulp, and Tucek, 1956), indicate that the last major cold maximum in this part of the continent occurred about 12,000 years ago, a time probably coinciding with the maximum advance of the last continental ice sheet in western North America.

Museum of Natural History  
University of Oregon, Eugene

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### THE GENUS *COLLINSIA*. III. THE SIGNIFICANCE OF CHIASMATA FREQUENCIES AS A CYTOTAXONOMIC TOOL<sup>1</sup>

E. D. GARBER

The genus *Collinsia* Nutt. (Scrophulariaceae) includes twenty-one recognized species, divided into two groups (Newsom, 1929; Pennell, 1951). The species in one group have "sessile" flowers congested in whorls, with pedicels shorter than to no longer than the calyces of the lower whorls, and with flat, mature seeds. The species in the other group have pedicelled flowers, either solitary or in whorls, with the pedicels of the flowers of the lower whorls from as long as to longer than the calyces, and with either flat or thick, mature seeds. There are other differences between the species in these two groups but they are not as clear as those which have been mentioned. The basic chromosome number for the genus is 7; no polyploid species have yet been found (Garber, 1956, and unpubl.).

The species in each of the two groups apparently differ in their mean number of chiasmata per bivalent at metaphase I. With the exception of *C. corymbosa* Herder, the species with "sessile" flowers have mean values of 1.1-1.5 and the species with pedicelled flowers, 1.7-1.9 (Garber, 1956). *Collinsia corymbosa* was placed in the species group with "sessile" flowers by both Newsom (1929) and Pennell (1951), yet its combination of characters shows it to be somewhat intermediate between these two groups of species (Garber and Gorsic, 1956). The flowers are borne in dense, capitate whorls on pedicels 3-7 mm. long, with calyx lobes approximately 5 mm. long, and the mature seeds are thick. The mean number of chiasmata per bivalent at metaphase I in *C. corymbosa*, however, has been found to be 1.7-1.8, a value characteristic of the group of species with pedicelled flowers.

This paper presents evidence regarding the validity of chiasma frequency as a cytotaxonomic tool in studying relationships among species of *Collinsia* by considering the chromosome associations and aberrations

<sup>1</sup> This investigation was aided by grants from the National Science Foundation and the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.

in interspecific hybrids involving *C. heterophylla*, a species with “sessile” flowers.

TABLE 1. A comparison of certain morphological characters of *C. corymbosa*, *C. heterophylla*, and their interspecific hybrids (hcy 56632).

Character	Character <i>C. heterophylla</i>	Interspecific hybrid	<i>C. corymbosa</i>
Flower, position	“sessile”	<i>corymbosa</i> -like	“sessile”
Flower, upper lobes, length	prominent	intermediate	rudimentary
Flower, upper lobes, markings	present	present	absent
Flower, lateral lobes, color	blue-red	segregating*	cream white
Flower, tube color	pale blue-red	light blue	light blue
Flower, upper stamen filaments	basal spurs	no basal spurs	no basal spurs
Calyx lobes	glabrous	hairy, glandular	hairy, glandular
Leaf petiole	short	long	long

\* Pale or light blue.

MATERIALS AND METHODS

For the current studies, plants were grown from seed which was kindly supplied by Dr. R. Bacigalupi. Of the species involved, *C. corymbosa* is apparently restricted to the area around Fort Bragg, Mendocino County, California; *C. heterophylla* Buist, typical of the group with “sessile” flowers, may be found throughout the hilly portions of the western regions of California from the extreme south almost to the Oregon boundary; *C. sparsiflora* Fisch. and Mey., representative of the pedicelled group, occurs at low and middle elevations northward in the California coast ranges from Marin County and in the Sierra Nevada from Tuolumne County to Butte County.

Clusters of buds were fixed in a solution (6:3:2) of methanol, chloroform, and propionic acid (Pienaar, 1955), which proved superior to the familiar alcohol-acetic acid fixative, and the buds were then stored in a deep freezer until needed. Smears of pollen mother cells were stained with acetocarmine. Pollen grains were stained with basic fuchsin in lactophenol.

HYBRIDIZATION RESULTS

Interspecific hybridizations involving “sessile”-flowered *C. heterophylla* and *C. corymbosa* were easily accomplished. The yield and quality of the resulting seeds were excellent and approximately 90 per cent of the seeds germinated. Interspecific hybridizations involving the pedicelled-flowered species *C. sparsiflora* and *C. corymbosa*, however, were almost completely unsuccessful.

TABLE 2. Chromosome configurations at metaphase I in interspecific hybrids (hcy 56632) between *C. corymbosa* and *C. heterophylla*.

II	I	III	IV	Plant No.			
				3	5	6	10
7	....	....	....	14	48	42	19
6	2	....	....	19	15	61	18
5	4	....	....	12	4	24	18
4	6	....	....	2	....	4	4
3	8	....	....	....	....	2	....
5	1	1	....	1	2	....	1
4	3	1	....	....	....	1	....
3	5	1	....	1	....	1	....
5	....	....	1 chain	....	1	2	1
5	....	....	1 ring	....	....	....	1
4	2	....	1 chain	....	....	1	2
4	2	....	1 ring	....	1	....	1
3	4	....	1 chain	....	1	....	1
No. of pollen mother cells				49	72	138	66

MORPHOLOGICAL STUDIES. Only the interspecific hybrids between *C. heterophylla* and *C. corymbosa* were studied. The morphological differences between these species are so obvious that there is no difficulty in distinguishing these species. Certain characteristics of each species and their hybrids are summarized in Table 1.

In general, the interspecific hybrids resembled *C. corymbosa* in their vegetative characteristics, but the flowers were more like those of *C. heterophylla*. The hybrids were intermediate in height but almost as tall as *C. heterophylla*.

CYTOLOGY. The chromosome associations at metaphase I in the interspecific hybrids are summarized in Table 2. Most pollen mother cells had univalents and bivalents. A few pollen mother cells also had a trivalent or a quadrivalent. The mean number of chiasmata per bivalent at metaphase I in pollen mother cells with only bivalents was 1.3–1.4, which were the values observed for hybrids between *C. heterophylla* and *C. sparsiflora* (Garber and Gorsic, 1956).

No pollen mother cells had two trivalents or two quadrivalents. Since many pollen mother cells had univalents, it was conceivable that a ring of six chromosomes, the result of two reciprocal translocations involving one chromosome, could have been formed. Several configurations make this interpretation unlikely. The conclusion that at least a single heterozygous reciprocal translocation occurred in the interspecific hybrid appears to be reasonable. Pollen mother cells at telophase I often displayed a dicentric chromatid bridge and a very small fragment; a few cells had two bridges and two very small fragments (Table 3). These observations indicate that the interspecific hybrids had two heterozygous paracentric inversions.



TABLE 3. Number of pollen mother cells with dicentric chromatid bridges and fragments at telophase I in interspecific hybrids between *C. corymbosa* and *C. heterophylla*.

Plant No.	No. of bridges + fragments			No. of pollen mother cells
	0	1	2	
5	55	24	4	83
6	50	27	2	79
10	73	31	7	111

STERILITY. The interspecific hybrids were almost completely pollen-sterile, with less than 0.3 per cent stainable pollen grains. No seeds were set even when the flowers were hand-pollinated.

#### DISCUSSION

The group with "sessile" flowers includes the following species: *C. heterophylla*, *C. concolor*, *C. tinctoria*, *C. bartsiaefolia*, *C. multicolor*, *C. austromontana*, and *C. corymbosa* (Pennell, 1951). It has been possible to assemble data on the crossability, the fertility, and chromosome associations in interspecific hybrids involving *C. heterophylla*, *C. concolor*, *C. tinctoria*, and *C. bartsiaefolia* as well as in interspecific hybrids between *C. sparsiflora* and both *C. heterophylla* and *C. concolor* (Garber, unpub.; Garber and Gorsic, 1956; Hiorth, 1933).

When hybrids can be made between species, intragroup hybrids are more difficult to accomplish than intergroup hybrids, the yield of germinating seeds being much greater for the intergroup hybrids. Intragroup hybrids involving species with "sessile" flowers were fertile to some degree; intergroup hybrids were completely sterile. The hybrids between *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

Intragroup hybrids involving species with "sessile" flowers displayed only bivalents at metaphase I; intergroup hybrids had such chromosomal aberrations as heterozygous reciprocal translocations and heterozygous paracentric inversions. These chromosomal aberrations were responsible for the complete sterility of the intergroup hybrids. In this respect also, the hybrids involving *C. corymbosa* and *C. heterophylla* behaved as intergroup hybrids.

It seems reasonable to assume that barriers to hybridization have occurred for the species within the group with "sessile" flowers. Since such hybrids are fertile to some degree, such barriers would minimize the possibility of large scale introgression. The complete sterility of hybrids between species of different groups which easily hybridize serves as an effective barrier against introgression.

It is not yet clear what significance may be attached to the observation that hybrids between *C. corymbosa* and *C. heterophylla* have a mean number of chiasmata per bivalent at metaphase I of 1.3-1.4, a value also found in the interspecific hybrids involving *C. sparsiflora* and both *C.*

*heterophylla* and *C. concolor*. It is possible that this observation may be related to the length of the homologous segments in the chromosomes of the species in different groups.

Although the evidence may be interpreted to indicate that *C. corymbosa* does not belong with the species having "sessile" flowers, it appears more reasonable at this time to consider that *C. corymbosa* does not belong to the group of species including *C. heterophylla*, *C. concolor*, *C. tinctoria*, and *C. bartsiaefolia*. The other two species with "sessile" flowers, *C. multicolor* and *C. austromontana*, may yield critical information on this point. At any rate, the differences in the mean number of chiasmata per bivalent at metaphase I appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*. It must remain for future investigation to determine the extent to which this tool may be used.

#### SUMMARY

Interspecific hybridizations between *C. corymbosa* and *C. heterophylla* were easily accomplished, yielding a very high percentage of germinating seeds. The hybrids were completely sterile. Different numbers of bivalents and univalents were observed at metaphase I and, occasionally, a trivalent or quadrivalent was seen at the same stage. The multivalent was interpreted as a heterozygous reciprocal translocation. One or two dicentric chromatid bridges plus one or two very small fragments were observed at telophase I, indicating the presence of at least two heterozygous paracentric inversions. The combined data indicated that *C. corymbosa* does not belong with a number of species with "sessile" flowers but did not conclusively demonstrate that this species does not belong within the group of species having "sessile" flowers. The results indicate that differences in chiasma frequency appear to have cytotaxonomic value in studying relationships among the species of *Collinsia*.

The author is indebted to Mr. J. Gorsic for his technical assistance and to Dr. G. L. Stebbins for reading the manuscript.

Department of Botany,  
The University of Chicago  
Chicago, Illinois

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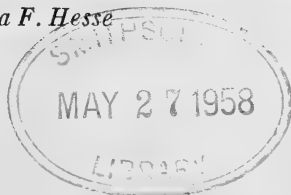
A WEST AMERICAN JOURNAL OF BOTANY

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# MADRÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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THE PHYLOGENETIC DIVISION OF THE SUBFAMILY  
CEREIOIDEAE, CACTACEAE<sup>1</sup>

FRANZ BUXBAUM

The subfamilies Pereskioideae K. Schum. and Opuntioideae K. Schum. of the family Cactaceae Lindl. are fairly well understood, but the subfamily Cereioideae K. Schum. (Schumann, 1898 and 1903) is so large and complex that its subdivision has puzzled all authors. The main reason for this difficulty in the past was that the descriptions of practically all genera belonging to this subfamily were completely inadequate. The internal structure of flowers, fruits, or seeds, all of extreme importance in recognizing relationships in the Cactaceae, had not been sufficiently examined. Thus all former attempts to subdivide this subfamily resulted in more or less schematic divisions which cut across the lines of evolution and united members of very different origin into polyphyletic units.

Therefore my first approach to this extremely difficult problem was a survey of the morphology of the Cactaceae (Buxbaum, 1936–1957c). These studies began with the more advanced branches of the Cereioideae. The more primitive genera were not at first available to me and their disposition remained very questionable. Nevertheless it was possible to delimit several of the tribes published by former authors as well as to point out the biphyletic origin of those cacti which Berger (1926) united into his Trichocerei. I discussed this provisional new phylogeny at the International Congress of the International Organization for Study of Succulent Plants (I.O.S.) at Zürich in 1951, and later this was published in provisional outline form (Buxbaum 1953a, 1956h). The details of the phylogeny of the tribe Echinocactae (Euechinocactineae) were first published in 1951 (Buxbaum 1951b, 1951c, 1951h).

Since then it has been possible at least to delimit the extent of the tribes, and, in some instances, to indicate probable evolutionary lines. Nevertheless, much study still will be necessary to obtain a final knowledge of the evolution of the Cereioideae. This is because, for the most part, recently described "new genera" are so carelessly and insufficiently described that it is impossible to accept them. Since the Congress at Zürich I have been asked so often for an amplification of "my system" that I feel it necessary to publish at least the emended, or new, tribes and subtribes in accordance with the International Code of Botanical Nomenclature. To do this strictly in accord with the Code, it is necessary, unfortunately, to substitute new and different names for many of my provisional ones, but in each such case I have indicated my provisional name as a *nomen provisiorium* in the synonymy.

<sup>1</sup>Part of the cost of publication of this manuscript has been defrayed by the Cactus and Succulent Society of California. The task of preparing the manuscript for publication was done principally by Dr. Helen Sharsmith of the Herbarium of the University of California, Berkeley.

It should be emphasized that the classification within the tribes in most cases is not yet elaborated definitively and that several genera still are of doubtful position. In addition, this publication does not intend to give any judgment with regard to the validity or invalidity of many of the genera published hitherto. This can be done only in more detailed studies.

In order to interpret correctly the descriptive terminology used herein, readers are referred to my publications in English on the morphology of Cacti (Buxbaum 1950b, 1953c, 1955), where the specialized usage of such terms as pericarpel, receptacle, etc., will be found.

Backeberg overloaded his "Systematische Übersicht" with Latin-named taxa. Thus, in his second edition (1942), for the entire family Backeberg included 189 genera under 178 taxa above the rank of genus; for the Cereoideae alone he included 172 genera in 147 higher taxa. None of these was given a Latin diagnosis; thus all are *nomina nuda*, although he sometimes gave a suitable description in German. Backeberg pointed out that these Latin names were used only instead of numbers of a key, giving a characteristic by name; thus they are not true taxa and, indeed, many of them are adjectival and occur several times in different parts of the "system." Nevertheless, in his first edition, Backeberg (1938) put his name as author behind each of his names.

These names are ignored here except those of tribes, subtribes, and "nationes." As they are all *nomina nuda*, they could all have been ignored. However, so far as the name of any of these corresponds to a taxon used here, it is cited in the synonymy.

Even Berger (1926) did not give any description to his "Sippen" as he was aware of their provisional character. These, also, are in part cited here.

## TRIBUS I.<sup>2</sup> *Leptocereae* trib. nov.

*Echinocacteae* K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose p.p. (1920), p. 1, Subtribe); *Leptocerei* Berg. nom. nud., p.p. (1926, p. 43, 95, Sippe); *Pfeifferae* Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe); *Trichocerei* Berg. nom. nud., p.p. (1926, p. 49, 96, Sippe); *Leocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 42, Natio); *Cephalocerei* Backeb. nom. num., p.p. (1938, Sippe; 1942, p. 50, Natio); *Corryocerei* Backeb. nom. num., p.p. (1938, Sippe; 1942, p. 26, Natio); *Archicereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Archicereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

<sup>2</sup>The method of synonym citation used throughout this paper is as follows. Under each tribe are listed all synonyms pertinent to the tribe or to any of its subtribes or lineae. Each synonym is followed 1) by the author, 2) nomen nudum or nomen provisorium if applicable, 3) pro parte (p.p.) if the synonym applies only in part to the tribe in question, 4) the date and page, if any, of publication and rank of name (all in parentheses); for example: *Trichocerei* Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe). By referring to the "Literature Cited," which includes all authors listed in the synonymy, the complete reference may be obtained. Under each subtribe any tribal synonyms pertinent to the particular subtribe in question are repeated, and are designated p.p., nom. nud., or nom. prov. as necessary. The date of publication and rank, however, are not repeated, since this information is available in the full synonymy listed under each tribe. No synonymy has been included for the lineae except for Dr. Buxbaum's own applicable *nomina nuda* or *nomina provisoria*.—Ed.



Plantae habitu cereoideae modo primitivo ramosae nonnumquam prostratae vel adscendentes; costis plerumque haud numerosis, interdum 4 ad 8 iisque altis vel costis humilibus numerosis; floribus primitivissimis perianthio radiato parvo pericarpello et receptaculo perspicue cauliformibus brevibus squamis numerosis obsitis areolas spinosas, setosas vel saltem pilosas aut lanuginosas in axillis gerentibus. Genus typicum. *Leptocereus* (Berg.) Britt. & Rose.

Habit cereoid, the stems with branches arising basally or laterally and sometimes in a very primitive manner, sometimes prostrate or ascending; ribs usually few, sometimes only 4–8 and then very high, or numerous and low. Flowers very primitive; perianth radiate, relatively small; pericarpel and receptacle always shoot-like, short, the scales usually numerous and with spiny, bristly, or at least hairy or woolly areoles in their axils. South and Central America.

Genera (included for the present). *Armatocereus* Backeb., *Corryocactus* Britt. & Rose, *Erdisia* Britt. & Rose, *Eulychnia* Phil. (incl. *Philippicereus* Backeb.), *Facheiroa* Britt. & Rose (incl.? *Thrixanthocereus* Backeb. and ?*Vatricania* Backeb.), *Leocereus* Britt. & Rose, *Leptocereus* (Berg.) Britt. & Rose, *Neoraimondia* Britt. & Rose (incl. *Neocardenasia* Backeb.), *Neoabbottia* Britt. & Rose, *Samaipaticereus* Card., *Zehntnerella* Britt. & Rose.

This tribe contains several genera of very primitive character, especially with very primitive flowers. As these genera have not yet been examined sufficiently, it is not yet possible to arrange them phylogenetically. Some of the genera may possibly be transferred into one of the advanced tribes after further study. This tribe doubtless contains the oldest genera of the Cereoideae. The genus *Leptocereus* is probably the oldest of them.

## TRIBUS II. **Hylocereae** trib. nov.

*Rhipsalideae* DC. (1828, p. 475, Tribus); *Echinocacteae* K. Schum, p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Hylocereanae* Britt. & Rose (1920, p. 183, Subtribe); *Epiphyllanae* Britt. & Rose (1923, p. 177, Subtribe); *Rhipsalidanae* Britt. & Rose (1923, p. 208, Subtribe); *Epiphyllaeae* Berg. nom. nud. (1926, p. 30, 95, Subtribus); *Hylocereae* Berg. nom. nud. (1926, p. 32, 95, Subtribus); *Leptocerei* Berg. nom. nud., p.p. (1926, p. 32, 95, Sippe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Pachycerei* Berg. nom. nud., p.p. (1926, p. 59, 97, Sippe); *Pfeifferae* Berg. nom. nud., p.p. (1926, p. 42, 95, Sippe); *Corryocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 26, Natio); *Heliocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 45, Natio); *Nyctohylocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 24, Natio); *Heliohylocerei* Backeb. nom. nud. 1938, Sippe; 1942, p. 25, Natio); *Strophocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 24, Natio); *Phyllocacti* Backeb. nom. nud. (1938, Sippe; 1942, p. 23, Natio); *Phyllocactinae* Backeb. nom. nud. (1942), p. 23, Subtribus); *Hylocereideae* F. Buxb. nom. prov. (1953a, p. 6, Tribus); *Hylocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus); *Hylocereinae* F. Buxb. nom. prov. (1953a, p. 6, Subtribus); *Hylocereineae* F. Buxb. nom. prov. (1956h, System 2, Subtribus); *Wittiae* F. Buxb. nom. prov. (1953a, p. 6, Linea); *Archirhipsalidae* F. Buxb. nom. prov. (*ibid.*, Linea); *Zygocacti* F. Buxb. nom. prov. (*ibid.*, Linea); *Eurhipsalidae* F. Buxb. nom. prov. (*ibid.*, Linea).

Frutices terrestres vel epiphytici multum ramosi arcuati adscendentes penduli vel scandentes; ramis paulum stabilibus teretibus costis numerosis humilibus, saepius costis paucis altis vel ramis trialatis vel phyllocladioides vel teretibus ecostatisque, saepe articulatis; areolis apud genera primitiva spinosis, apud ea deductissima paulum modo lanuginosis; podariis plerumque rudimenta laminae gerentibus saepe glandulis nectariferis instructis; floribus ex areolis lateralibus saepe numerosissimis vel ex areolis ad apicem ramorum aggregatis, maximis aut minimis, nocturnis vel diurnis, albis, lutescentibus, viridescentibus, roseis vel coloratis, infundibuliformibus vel rotatis vel tubulatis plerumque radiatis, saepe receptaculo curvato pseudozygomorphis (apud *Zygocactus* vere zygomorphis); pericarpello apud genera primitiva squamoso et spinoso vel post anthesin spinas formante, apud genera deducta squamoso sine areolis, apud genera deductissima nudo; receptaculo breviter vel elongatissime infundibuliformi (apud subtribus *Rhipsalinas* paene absente) spinoso vel tantum squamoso vel plus minusve nudo, squamis receptaculi et pericarpelli saepe glanduliferis; perianthio plerumque conspicuo interdum basi eius tubum perianthii formante; staminibus fauce et tubo receptaculi modo variabili instructis numerosis vel reductione receptaculi paucis; pistillo crasso ramis stigmaticis permultis nonnumquam capitate cohaerentibus; funiculis ramosis (rarius simplicibus) saepe papillosis; fructu spinoso vel gibboso vel nudo laevique uviformi; seminibus magnis (apud *Nyctocereum* maximis) usque ad minimis, testa laevi vel foveolis interstitialibus punctata, perispermio absente, hypocotyle embryonis tenero, cotyledonibus magnis. Genus typicum. *Hylocereus* (Berg.) Britt. & Rose.

Shrubs of terrestrial habit, or in advanced genera shrubs of epiphytic, weak habit, then arching upward or leaning, hanging, or climbing, and much branched basally and laterally; branches sometimes terete with many low ribs or more frequently with only a few high ribs, or 3–5-angled to phylloclade-like, or sometimes terete and without ribs; both phylloclades and terete branches often articulate; branches usually developing aerial roots; areoles in primitive genera spiny, in advanced genera with only a little felt or a few hairs; podaria mostly with rudiments of laminae, often with an extranuptial nectary at the base of the lamina rudiment; cortical tissue with an abundance of large mucilaginous cells. Flowers lateral, often several from an areole which flowers repeatedly, or from aggregations of areoles at the tops of joints, very large (especially in subtribe *Hylocereinae*) to very small (subtribe *Rhipsalinae*, lineae *Rhipsalis*), night-blooming and white, pinkish, or yellowish, or day-blooming and bright colored to sometimes inconspicuous white, greenish, or yellowish, funnelliform to widely rotate or tubular, radiate or sometimes pseudozygomorphic by bending of the receptacle (in *Zygocactus* zygomorphic); pericarpel in the more primitive genera scaly and spiny, in somewhat more advanced genera developing spines at maturity, in the more advanced genera without areoles, and finally in the most advanced genera nude and terete; receptacle in some primitive genera with spiny areoles in the

axils of scales, in the more advanced genera sometimes with very large scales, or in the most advanced genera more or less nude (scales when present very often with nectar glands below apex), short and massive-funnelform, or by extension of internodes very long (especially in *Epiphyllum*), in the subtribe *Rhipsalinae* reduced or almost totally absent, some of the most highly evolved genera with a true perianth tube; stamens variously distributed in the throat and along walls of the receptacle, sometimes only in upper part of the receptacle (*Epiphyllum*), sometimes a separate group around the pistil, mostly very numerous, fewer in the species with greatest reduction of receptacle, sometimes as few as 6 (*Rhipsalis cassytha* Gaertn.); style often very robust, the stigma lobes sometimes branched, usually numerous but sometimes in the most advanced genera few and small, or the stigma subcapitate; ovules arranged in bunches on branched funicles, these often bearing stiff papillae at the inner side of the bend (in the most advanced genera the funicles short and simple). Fruits fleshy, in the primitive genera with spines sometimes very numerous but fine, in the more advanced genera humped by the podaria of the scales, in the most advanced genera smooth and berry-like. Seeds very large (*Nyctocereus*) to very small (*Rhipsalinae*), smooth or spotted, without perisperm; embryo with large cotyledons and slender hypocotyl. Tropical and subtropical North, Central, and South America and West Indies, some *Rhipsalis* species secondarily distributed in tropical Africa, Madagascar, Zanzibar, Comoro Islands, and Ceylon.

#### SUBTRIBUS 1. *Nyctocereinae* subtrib. nov.

*Echinocactae* K. Schum., p.p.; *Cereanae* Britt. & Rose, p.p.; *Nyctocerei* Berg. nom. nud., p.p.; *Leptocerei* Berg. nom. nud., p.p.; *Pachycerei* Berg. nom. nud., p.p.; *Corryocerei* Backeb. nom. nud., p.p.; *Heliocerei* Backeb. nom. nud., p.p.; *Heliohylcerei* Backeb. nom. nud.

Frutices terrestres ramis minus stabilibus vel arbores (*Dendrocereus*) ramosae, ramis alatis costis 3–5 altissimis vel eis humilibus teretibusque numerosis: floribus albis nocturnis (apud lineam *Heliocerei* rubris diurnis), pericarpello et plerumque etiam receptaculo spinosis (apud lineam *Harrisiae* tantum pilosis) radiatis (apud *Aporocactus* pseudozygomorpha), receptaculo tubiformi vel infundibuliformi. Genus typicum. *Nyctocereus* (Berg.) Britt. & Rose.

Habit terrestrial, the stems branching from the base or above; branches weak, or, if tree-like (as in *Dendrocereus*), partly pendent, terete with numerous low ribs or 3–alate with high ribs. Flowers usually night-blooming and white, sometimes (Linea *Heliocerei*) day-blooming and bright red, mostly radiate, rarely (in *Aporocactus*) somewhat zygomorphic; receptacle tubular to funnelform; areoles of pericarpel and receptacle usually spiny, sometimes (Linea *Harrisiae*) with hairs only.

#### LINEA A. *Nyctocerei* linea nov.

Flores primitivissimi receptaculo et pericarpello spinosis. Genus typicum. *Nyctocereus* (Berg.) Britt. & Rose.

Flowers white, very primitive; pericarpel and receptacle very spiny.

Genera. *Nyctocereus* (Berg.) Britt. & Rose, *Brachycereus* Britt. & Rose and *Peniocereus* (Berg.) Britt. & Rose.

**LINEA B. *Acanthocerei* linea nov.**

Flores magni, infundibuliformes, albi, pericarpello spinoso, receptaculo haud, vel in parte basali tantum spinoso. Genus typicum. *Acanthocereus* (Berg.) Britt. & Rose.

Flowers large, funnellform, white; pericarpel spiny; receptacle with spines only in basal part.

Genera. *Acanthocereus* (Berg.) Britt. & Rose, *Dendrocereus* Britt. & Rose.

**LINEA C. *Harrisiae* linea nov.**

Flores magni, infundibuliformes, albi, areolis pericarpelli et receptaculi pilosis non spinosis. Genus typicum. *Harrisia*. Britt.

Flowers large, funnellform, white; areoles of pericarpel and receptacle with hairs only.

Genera. *Harrisia* Britt., *Eriocereus* (Berg.) Ricco.

**LINEA D. *Heliocerei* linea nov.**

Flores diurni, rubri (exceptionibus paucis albis), magni, radiati vel positione staminum et receptaculo curvato pseudozygomorphi, pericarpello et receptaculo spinulosis. Genus typicum. *Heliocereus* (Berg.) Britt. & Rose.

Flowers day-blooming, red or (in one taxon) white, large, radiate to pseudozygomorphic by position of the stamens and/or bending of the receptacle; pericarpel and receptacle with fine spines.

Genera. *Heliocereus* (Berg.) Britt. & Rose, *Aporocactus* Lem.

**SUBTRIBUS 2. *Hylocereinae* Britt. & Rose emend.**

*Echinocactae* K. Schum, p.p.; *Hylocereanae* Britt. & Rose; *Epiphyllanae* Britt. & Rose, p.p.; *Hylocereae* Berg. nom. nud.; *Epiphyllae* Berg. nom. nud., p.p.; *Nyctohylocerei* Backeb. nom. nud.; *Strophocerei* Backeb. nom. nud.; *Phyllocacti* Backeb. nom. nud., p.p.

Frutices ramosi elongati saepe scandentes, interdum repentes saepe epiphytici, ramis, angulatis vel alatis vel costatis rarius teretibus, radices aereas emittentibus; areolis plerumque spinosis; floribus magnis albis interdum roseis, pericarpello et receptaculo saepe crassissimis spinulosis squamosis interdum areolis solum pilosis, apud *Hylocereum* squamosis nudisque; perianthio radiato; fructu carnoso interdum permagno. Genus typicum: *Hylocereus* (Berg.) Britt. et Rose.

Habit elongated, vine-like, climbing, trailing or pendent, the stems branched, both stems and branches ribbed, fluted, or rarely flat, the joints emitting aerial roots, the areoles usually spiny. Flower mostly large, white or rarely pinkish; receptacle and pericarpel spiny and scaly, rarely the areoles bearing only a few hairs and wool, rarely without areoles (in *Hylocereus*); perianth limb regular. Fruit a fleshy, often large berry with a pulp, usually bursting upon maturity.

Genera. A. *Selenicereus* (Berg.) Britt. & Rose, *Cryptocereus* Alex., *Deamia* Britt. & Rose, *Strophocactus* Britt. & Rose. B. *Mediocactus* Britt. & Rose, *Wilmattea* Britt. & Rose, *Hylocereus* (Berg.) Britt. & Rose. C. *Werckleocereus* Britt. & Rose, *Weberocereus* Britt. & Rose, *Eccremocactus* Britt. & Rose. *Aporocactus* is now assigned to subtribe Nyctocereinae, linea Heliocerei.

No formal division into lines is proposed here, although the genera of this subtribe can be divided into three groups of presumably more or less closely related genera (A, B, C in list of genera above). When these genera are better known a formal subdivision may be possible. However, as Kimnach and Hutchison (1957) have pointed out, several of these genera may have to be reduced.

### SUBTRIBUS 3. EPIPHYLLINAE Britt. & Rose emend.

*Epiphyllanae* Britt. & Rose, p.p.; *Epiphylleae* Berg. nom. nud., p.p.; *Phyllocacti* Backeb. nom. nud., p.p.

Frutices epiphytici nonnumquam scandentes phyllocladiis variabilibus, eis saepe ex ramis non succulentis orientibus; floribus magnis radiatis nocturnis; receptaculo maxime elongato paulum squamoso, pericarpello squamoso, areolis in axillis squamarum interdum pilosis. Genus typicum. *Epiphyllum* Haw.

Habit epiphytic or climbing, with phyllodes of very variable shape, these sometimes branching from non-succulent shoots. Flowers conspicuous, radiate, night-blooming; pericarpel scaly, sometimes with hairs in the axils of the scales; receptacle much elongated, bearing only a few scales.

Genera. *Epiphyllum* Haw. (including *Marniera* Backeb.). Other genera included originally by Britton and Rose are here transferred to Hylocereinae, Disocactinae, and Rhipsalinae. See also Kimnach and Hutchison (1957).

### SUBTRIBUS 4. Disocactinae subtrib. nov.

*Epiphyllanae* Britt. & Rose, p.p.; *Epiphylleae* Berg. nom. nud., p.p.; *Phyllocacti* Backeb. nom. nud., p.p.; *Wittiae* F. Buxb. nom. prov.

Frutices epiphytici phyllocladiis saepe ex ramis non succulentis orientibus; floribus magnis vel maxime simplicatis diurnis conspicue coloratis radiatis vel pseudozygomorphis; receptaculo tubulato vel infundibuliformi, plerumque squamoso, interdum petaloideo et in tubum perianthii transeunte; pericarpello squamoso vel fere nudo. Genus typicum. *Disocactus* Lindl.

Habit epiphytic, the phyllodes often branching from non-succulent shoots. Flowers large in some genera, and much simplified in others, day-blooming, bright colored, regular or pseudozygomorphic by bending of the receptable; pericarpel scaly to nearly naked; receptacle tubular to funnel-form, mostly with scales, sometimes petaloid and transitional to a perianth tube.

Genera. *Nopalxochia* Britt. & Rose, *Lobeira* Alex., *Bonifazia* Standl. & Steyerl., *Chiapasias* Britt. & Rose, *Disocactus* Lindl., *Pseudorhipsalis* Britt. & Rose, *Wittia* K. Schum. *Lobeira* and *Bonifazia* will probably be reduced to *Nopalxochia* eventually. Kimmach and Hutchison (1957) reduce *Lobeira* to *Nopalxochia*.

#### SUBTRIBUS 5. RHIPSALINAE Britt. & Rose emend.

*Rhipsalideae* DC.; *Rhipsalidanae* Britt. & Rose; *Pfeifferae* Berg. nom. nud., p.p.; *Epiphyllloides* Backeb. nom. nud.; *Eurhipsalidae* F. Buxb. nom. prov.

Frutices epiphytici, rarissime terrestres, saepe radicanes, ramis angulatis, phyllocladioideis vel teretibus (in species unica opuntioideis) saepe articulatis; areolis lateralibus vel partim (interdum omnibus) aggregationem pseudoterminalem (pseudoareolam) formantibus; floribus ex areolis lateralibus vel ex aggregatione areolarum orientibus, diurnis, albidis lutescentibus vel coloratis, minimis, mediocribus, vel conspicuis, rotatis vel subinfundibuliformibus radiatis, in genere *Zygocactus* tantum zygomorphis; receptaculo plerumque brevissimo vel absente, pericarpello squamoso vel nudo, tereti vel anguloso, rarissime areolis setaceo-aculeatis instructo; foliis perianthii nonnumquam tubum perianthii formantibus; fructibus baccatis, seminibus parvis elongatis, hilo magno basali, embryonis cotyledonibus magnis, perispermio deficiente. Genus typicum. *Rhipsalis* Gaertn.

Habit rarely terrestrial, mostly epiphytic, the stems very often bearing aerial roots; branches angular, flattened, terete, or (in one species) *Opuntia*-like, often articulate; areoles lateral on the branches or the uppermost areoles of each joint aggregated at the top of joint and forming a large pseudoterminal pseudoareole. Flowers arising at lateral areoles or from pseudoterminal pseudoareoles, very small to quite large, day-blooming, whitish, yellowish, or colored, rotate or somewhat funnelform, radiate or rarely (in *Zygocactus*) zygomorphic; perianth a true tube in some genera; pericarpel terete or angular, scaly or nude, only very rarely bearing areoles with setaceous spines or hairs; receptacle mostly very short or absent. Fruits berry-like, globose, subglobose, or somewhat angular; pericarpel sometimes hidden in the branch tissue through the early growth of fruit (in other cases free from time of flowering). Seeds small, elongated; hylum large, basal; cotyledons large, the perisperm lacking.

#### LINEA A. *Pfeifferae* linea nov.

*Archirhipsalidae* F. Buxb. nom. prov.

Ramis angulatis spinosis, haud articulatis; receptaculo brevissimo, pericarpello squamoso et spinoso, vel tantum squamoso. Genus typicum. *Pfeiffera* Salm-Dyck.

Branches angular, spiny, not distinctly articulate. Flower with receptacle much shortened; pericarpel spiny or scaly.

Genera. *Pfeiffera* Salm-Dyck, *Acanthorhipsalis* (K. Schum.) Britt. & Rose.

**LINEA B. Schlumbergerae** linea nov.

*Zygocacti* F. Buxb. nom. prov.

Frutices ramis articulatis teretibus vel phyllocladioideis rarissime ex parte angulatis in specie unica opuntioideis; areolis partim prope apicem articularum pseudoareolam formantibus; floribus ex pseudoareola orientibus (rare lateralibus), coloratis (rarissime albis), radiatis, in genere *Zygocacto* zygomorphis; pericarpello nudo; apud genus *Erythrorhipsalis* areolas pilosas gerente; receptaculo abbreviato apud genus *Zygocacto* in tubum perianthii transeunte. Genus typicum. *Schlumbergera* Lem.

Branches distinctly articulate, terete or flattened, rarely angular or (in one taxon) *Opuntia*-like, each joint bearing at the top an aggregation of areoles, these usually forming a large pseudoterminal pseudoareole. Flowers arising from pseudoterminal pseudoareoles, rarely also from lateral areoles, conspicuously colored, naked or (in *Erythrorhipsalis*) the pericarpel bristly; receptacle shortened or (in *Zygocactus*) forming a true perianth tube.

Genera. *Erythrorhipsalis* Berg., *Hatiora* Britt. & Rose (including *Pseudozygocactus* Backeb.), *Rhipsalidopsis* Britt. & Rose (including *Epiphyllopsis* Berg., invalid name), *Schlumbergera* Lem., *Zygocactus* K. Schum. (including *Epiphyllanthus* Berg.), (Buxbaum, 1957e).

**LINEA C. Rhipsalis** linea nov.

*Eurhipsalidae* F. Buxb. nom. prov. (1953a, p. 6, Linea.)

Ramis articulatis vel inarticulatis, teretibus vel phyllodioideis, rarius angulatis; floribus plerumque ex areolis lateralibus orientibus, radiatis, patenti-rotatis, minimis; receptaculo paene absente; pericarpello nudo. Genus typicum. *Rhipsalis* Gaertn.

Branches articulate or non-articulate, terete or flattened, rarely angular. Flowers usually from lateral areoles (if pseudoterminal then at the final joints of branches with very unequal joints), small to very small, regular, radiate; receptacle nearly absent.

Genera. *Rhipsalis* Gaertn., *Lepismium* Pfeiff.

The more natural a supergeneric taxon of advanced development is, i.e., the more it really corresponds to a widely branching part of the evolutionary tree, the less it is possible to give a "diagnosis" of it. Contrary to this, artificial taxa which are established with regard to "similarities" can easily be "defined," but very often these represent only equal stages of different branches rather than a phylogenetic unit. This is especially true for the tribe Hylocereae whose classification I have attempted above. In summary, it can be stated that although this tribe contains plants of extreme morphological differences [such as *Mediocactus megalanthus* (K. Schum.) Britt. & Rose with its gigantic flowers and *Rhipsalis cassytha* Gaertn. with the smallest flowers known in the family], it is nevertheless a very clear phylogenetic unit. Doubtless separating very early in evolution, probably from *Leptocereus*-like ancestors, this branch has taken a

very peculiar development, which has enabled it to occupy even the wet tropical zone. Some members have even reached the epiphytic stage.

In stem shape this tribe is dominated by two opposing tendencies: 1) the tendency towards diminution of the number of ribs, which may also become alate, so that the stems finally become phyllodes, and 2) the tendency towards total loss of ribs by confluence of low podaria into continuous cortical tissue, thus producing terete branches. Both of these tendencies can become manifest even at very different stages of evolution. For example *Werckleocereus imitans* Kimnach & Hutchison (1956) shows exactly the same pinnate habit of the phyllodes that occurs in *Cryptocereus anthonyanus* Alex. and in *Epiphyllum anguliger* (Lem.) Kelsey & Dayton. These three species of subtribe Hylocereinae are members of quite different lines of development within the subtribe, as already indicated. Terete branches occur in the very primitive genus *Peniocereus* (subtribe Nyctocereinae), in some species of *Weberocereus* (subtribe Hylocereinae), and finally in *Erythrorhopsis*, *Hattiora*, and *Rhipsalis* (subtribe Rhipsalinae). In the flower at least three tendencies can be recognized: 1) the development of long-tubed, night-blooming, sphingine flowers, 2) the development of brightly colored, day-blooming, hummingbird flowers, 3) reduction and simplification of flowers. This third tendency can occur in combination with either of the first tendencies or separately.

Berger (1926), who had not yet recognized the tendency toward reduction in cacti, interpreted the simplified flowers as the most primitive ones. Therefore he did not recognize the connections, and so separated his "Rhipsalideae K. Schum." and Epiphyllae Berger as two subtribes. Today we can recognize the direct connection from a part of Berger's Sippe Nyctocerei (of his subtribe Cereae Berger) through the primitive subtribe Hylocereinae (= Berger's subtribe Hylocereae) to the three derived subtribes Epiphyllinae, Disocactinae, and Rhipsalinae. It has been necessary also to consider the day-blooming Epiphyllinae as another separate subtribe (Disocactinae), inasmuch as my recent examinations have made it evident that these have a separate origin.

### TRIBUS III. **Pachycereae** trib. nov.

*Echinocacteae* K. Schum., p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Pachycerei* Berg. nom. nud. (1926, p. 59, 97, Sippe); *Gymnocerei* Berg. nom. nud., p.p. (1926, p. 55, 97, Sippe); *Pachycereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Pachycereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Arbores columnares permagnae simplices vel ramosae; floribus ex areolis immutatis vel ex pseudocephalio vel ex cephalio orientibus, radiatis, perianthio conspicuo vel parvo, albis vel rubescentibus interdum purpurascens; pericarpello plus minusve dense squamoso; axillis squamarum areolas lanuginosas, lanatas saepe setosas vel pilosas gerentibus, in generibus deductissimis axillis subnudis vel vere nudis; receptaculo pericarpello simili squamis decurrentibus plerumque minus quam pericarpello areolato; podariis squamarum pericarpelli et receptaculi saepe



nectar productentibus; staminibus infimis a basi receptaculi distantibus, protrusioni receptaculi saepe diaphragmam formante insertis, staminibus superioribus permultis tubo et fauce insertis; fructu saepe spinosissimo, plerumque longitudine irregulariter dehiscente. Genus typicum. *Pachycereus* (Berg.) Britt. & Rose.

Trees of large columnar habit, the trunk branching or simple. Flowers arising from normal areoles or from a pseudocephalum or cephalium, radiate, night-blooming or day-blooming; perianth conspicuous or small, white to reddish or purplish; pericarpel more or less densely scaly, areoles woolly, hairy, bristly, rarely spiny, but at least felted, only in the most advanced genera nearly or quite naked; receptacle similar to pericarpel, but the internodes elongated and thus the scales broadly decurrent and the areoles more reduced, podaria of scales very often producing nectar; lower stamens arising from a receptacular protrusion which often forms a diaphragm across the receptacular tube thus closing the nectar chamber; upper stamens numerous, arising from tube and throat of the receptacle. Fruit sometimes very spiny, bursting with irregular longitudinal splits. North America and Central America.

Genera (included for the present). *Pachycereus* (Berg.) Britt. & Rose, *Lemaireocereus* Britt. & Rose sensu lat. [including *Hertrichocereus* Backeb., *Isolatocereus* (Backeb.) Backeb., *Marginatocereus* (Backeb.) Backeb., *Neolemaireocereus* Backeb. (invalid name), *Polaskia* Backeb., *Ritterocereus* Backeb., *Stenocereus* (Berg.) Ricco.], *Neobuxbaumia* Backeb. emend. Dawson & F. Buxb. (Buxbaum, 1957a, cf. also Buxbaum, 1953b and 1954a), *Carnegiea* Britt. & Rose non Perkins, *Mitrocereus* (Backeb.) Backeb. (including *Backebergia* Bravo H.), *Cephalocereus* Pfeiff. [including *Haseltonia* Backeb., *Pilosocereus* Byles & Rowley (= *Pilocereus* K. Schum. non Lem.) p.p., Buxbaum, 1956f]. Genera incertae sedis: *Escontria* Rose and *Anisocereus* Backeb. These probably belong here.

This tribe has not yet been sufficiently studied. It cannot be maintained as circumscribed by Berger in his Sippe *Pachycerei*, and eventually must be emended further than is indicated in the preceding paragraphs. It is now clear that *Cephalocereus* Pfeiff., if interpreted as including only the two North American species *C. senilis* Pfeiff. and *C. Hoppenstedtii* K. Schum., certainly belongs here, also the newer genus *Neobuxbaumia* and at least a part of *Pilocereus* in the sense that Schumann used this name [*Pilocereus* K. Schum. non Lem. was proposed for conservation, but the proposal was rejected by the Nomenclature Committee of the International Botanical Congress. Byles and Rowley (1957) have recently proposed the name *Pilosocereus* to substitute for *Pilocereus* K. Schum. non Lem.]. According to my own studies (Buxbaum, 1956e), there is no strict necessity for separating the North American species of *Pilosocereus* from *Cephalocereus*, as they are closely related. Therefore these species are included here under *Cephalocereus*.

The characters upon which Backeberg based the descriptions of the

genera which he separated from *Lemaireocereus* are quite insufficient to establish these genera, and further research is necessary. As indicated above, these genera are here included under *Lemaireocereus*. My last observations have shown that even *Lemaireocereus* [with *L. hollianus* (Weber) Britt. & Rose as type species] probably will not be retained, but will be placed in synonymy under *Pachycereus*.

#### TRIBUS IV. CEREAE Britt. & Rose emend.

*Echinocactae* K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Gymnocerei* Berg. nom. nud., p.p. (as to "Cereoidei"; 1926, p. 55, 97); *Trichocerei* Berg. nom. nud., p.p. (1926, p. 49, 96, Sippe); *Cephalocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 50, Natio); *Gymnocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Gymnocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Frutices semierecti, arcuati interdum prostrati, saepius arbores columnares erectae ramosae vel simplices; costis multis vel paucis interdum solum 3–5; floribus aut ex areolis immutatis aut ex pseudocephalio aut ex cephalio orientibus nocturnis saepe magnis campanulatis vel infundibuliformibus; pericarpello et receptaculo squamosis, squamis decurrentibus; axillis squamarum nudis (genere *Jasminocereus* excepto); staminibus infimis a basi receptaculi distantibus, plerumque protrusioni receptaculi diaphragmam non formante insertis, staminibus superioribus permultis tubo fauceque receptaculi insertis; fructibus carnosus dehiscentibus, funiculis seminum succosis. Genus typicum *Cereus* Miller.

Shrubs with slender half-erect, arching, or prostrate stems, varying to trees with large, columnar, upright stems, when trees the branches arising from the base, or from above a trunk, or the trunk simple; ribs many or few, sometimes (in some species of *Monvillea*) 3–5. Flowers arising from normal areoles or from a pseudocephalium or cephalium, nocturnal, radiate or somewhat bent and pseudozygomorphic, more or less slender-campanulate to funnellform, sometimes very large; pericarpel and receptacle bearing scales but lacking areoles in the scale axils (except in *Jasminocereus* which has a small amount of axillary felt which disappears on the fruit), in the more advanced genera the scales of pericarpel displaced upward onto the receptacle, the pericarpel thus becoming naked and showing only the decurrent scale bases; primary stamens arising above a distinct nectar chamber, but a diaphragm never formed; higher stamens arising from both wall and throat of the receptacle. Fruits fleshy, bursting, the funicles of the seeds juicy. South and Central America.

Genera. *Arrojadoa* Britt. & Rose non Mattf., *Austrocephalocereus* (Backeb.) Backeb. (including *Coleocephalocereus* Backeb., cf. Buxbaum, 1952b, c), *Browningia* Britt. & Rose (?including *Gymnanthocereus* Backeb.), *Cereus* Mill. [including *Monvillea* Britt. & Rose (cf. Werdermann, 1933), *Brasilicereus* Backeb., *Subpilocereus* Backeb.] *Jasminocereus* Britt. & Rose, *Stephanocereus* Berg., *Stetsonia* Britt. & Rose. Genera incertae sedis: *Lophocereus* (Berg.) Britt. & Rose and *Myrtillocactus* Cons. These probably belong here.

The study of this tribe is not yet completed. As it is now provisionally constructed it corresponds in general with the "Cereoidei" of Berger's Sippe *Gymnocerei*. Those genera which he lists in this Sippe as "Cactoidi" are now included in my Tribe VI, *Notocactaceae*. In addition I have included here the genus *Browningia*.

#### TRIBUS V. *Trichocereae* trib. nov.

*Echinocactaceae* K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Trichocerei* Berg. nom. nud., p.p. (1926, p. 49, 96, Sippe); *Cephalocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 50, Natio); *Lobiviae* Backeb. nom. prov. (1942, p. 32, Natio); *Austroechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 35, Natio); *Milae* Backeb. nom. nud. (1938, Sippe; 1942, p. 25, Natio); *Loxanthocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 27, Natio); *Trichocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Trichocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus); *Trichocerei* F. Buxb. nom. prov. (1953a, p. 5, Subtribus); *Rebutinae* Donald (1955, p. 84, Subtribe); *Trichocereineae* F. Buxb. nom. prov. (1956h, System 3, Subtribus); *Loxanthocerei* Buxb. nom. prov. (1949, p. 10; 1953a, p. 5, Subtribus); *Loxanthocereineae* Buxb. nom. prov. (1956h, System 3, Subtribus).

Cactaceae simplices vel ramosae, columnares erectae vel prostratae vel brevicolumnares vel globosae, permagnae usque ad pusillae, costatae vel costis plus minusve in tubercula divisae; floribus insignibus albis vel coloratis radiatis vel  $\pm$  pseudozygomorphis vel zygomorphis, receptaculo campanulato vel infundibuliformi vel tubiformi; pericarpello et receptaculo squamosis crispate pilosis (pericarpello rarissime spinuloso), apud genera deductissima pericarpello et receptaculo nudis; perianthio plerumque conspicuo, interdum (subtribus *Borzicactinae*) minuto sed receptaculo petaloideo-colorato; staminibus infimis prope basim receptaculi vel supra cameram nectariferam vel protrusione receptaculi insertis, interdum in pilos vel squamas staminodiales transformati, staminibus secundariis parte inferiore et fauce receptaculi insertis, rarius in fauce absentibus; fructibus semisuccosis vel siccis lateraliter vel circumscisso dehiscentibus, interdum non dehiscentibus sed desintegrescentibus; seminibus testae typo verrucoso, apud genera deducta saepe testa laevi foveolis interstitialibus punctata, habitu variabilibus. Genus typicum. *Trichocereus* (Berg.) Ricco.

Stems simple or branching, globular to columnar, erect to prostrate but not climbing, large to dwarfish; stems and branches ribbed, in the most advanced genera the ribs more or less divided into tubercles. Flowers conspicuous, white or colored, radiate or (in *Borzicactinae*) more or less zygomorphic; perianth conspicuous or (in some *Borzicactinae*) small with scale-like segments, but then the receptacle petaloid and colored; pericarpel and receptacle with numerous usually acuminate scales, the axils with wool and crisped long hairs or occasionally with fine spines but then these only on the pericarpel, in the most advanced taxa the pericarpel and receptacle naked; receptacle campanulate to funnelliform or

tubular; primary stamens inserted variously: 1) near receptacle base, leaving only a small nectar-furrow below, or 2) inserted at various heights so that the nectar chamber is limited indistinctly ("diffuse nectar chamber"), or 3) inserted on a more or less distinct protuberance which forms a closed nectar chamber; or the primary stamens sometimes transformed into staminodial hairs or scales; secondary stamens inserted only in lower part of tube and at margin of the receptacle, forming there a "hymen" which is absent only in the most advanced flowers. Fruits dry-fleshy, bursting laterally or opening with a circumscissile split or sometimes merely disintegrating. Seeds verrucose, in the highly advanced genera secondarily smooth and spotted, very variable in shape. South America.

This tribe is distinguished from the Tribe Notocacteae by 1) the stamen arrangement and 2) the basitony of the receptacular areoles (bristles never arise near the margin of the receptacle). Possibly it has developed from common ancestors with the Notocacteae, but its origin is not yet clear. The species descriptions are inadequate and consequently the genera are not yet sufficiently well defined; certainly several of the genera will be reduced to synonymy eventually.

#### SUBTRIBUS 1. *Trichocereinae* subtrib. nov.

*Echinocacteae* K. Schum. p.p.; *Cereanae* Britt. & Rose, p.p.; *Echinocereanae* Britt. & Rose, p.p.; *Nyctocerei* Berg. nom. nud., p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Cephalocerei* Backeb. nom. nud., p.p.; *Lobiviae* Backeb. nom. prov., p.p.; *Austroechinocacti* Backeb. nom. nud., p.p.; *Trichocerei* F. Buxb. nom. prov.; *Trichocereinae* F. Buxb. nom. prov.

Plantae magnae columnares simplices vel ramosae, rarius globosae; floribus magnis radiatis campanulatis vel plus minusve infundibuliformibus, plerumque albis vel albidis nonnumquam coloratis; perianthio magno; camera nectarifera praesente vel absente. Genus typicum. *Trichocereus* (Berg.) Ricco.

Stems large and columnar or rarely globular. Flowers radiate, campanulate to funnelform; perianth large, mostly white or whitish, sometimes brightly colored; nectar chamber lacking or present; stamen insertion beginning at base of the receptacle or above a nectar chamber.

Genera. *Trichocereus* (Berg.) Ricco. (including *Helianthocereus* Backeb., *Leucostele* Backeb., *Roseocereus* Backeb., and *Weberbauerocereus* Backeb.), *Echinopsis* Zucc. [including *Pseudolobivia* (Backeb.) Backeb.; cf. Buxbaum, 1956f], *Haageocereus* Backeb. (including *Neobinghamia* Backeb. and *Peruvocereus* Akers, cf. Buxbaum 1952a), *Arthrocereus* Berg. [including *Setiechinopsis* (Backeb.) de Haas], *Espostoa* Britt. & Rose (including *Pseudoespostoa* Backeb.); cf. Buxbaum, 1952b, c), *Soehrensia* Backeb., *Acanthocalycium* Backeb.

#### SUBTRIBUS 2. *Rebutinae* Donald emend.

*Echinocacteae* K. Schum. p.p.; *Echinocereanae* Britt. & Rose, p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Lobiviae* Backeb. nom. prov., p.p.; *Milae* Backeb. nom. nud.; *Rebutinae* Donald.

Plantae parvae vel pusillae, floribus radiatis, infundibuliformibus, coloratis (nonnullis albis exceptis); perianthio magno; receptaculo squamoso piloso, rarissime squamoso nudoque; pericarpello nonnumquam setaceo-spinuloso. Genus typicum. *Rebutia* K. Schum.

Plants small to dwarfish, flowers small, funnelform, radiate; perianth large, conspicuously colored or rarely whitish; pericarpel sometimes with small bristle-like spines; receptacle variously scaly, with hairs in the scale axils, or (in *Rebutia* K. Schum. subgen. *Rebutia*) the receptacle naked.

Genera (included for the present). *Lobivia* Britt. & Rose sensu lat. (including *Acantholobivia* Backeb., *Hymenorebutia* Frič ex Buin., *Sulcorebutia* Backeb.), *Rebutia* K. Schum. [including *Aylosteria* Speg., *Cylindrorebutia* Frič & Kreuz (invalid), *Digitorebutia* Frič & Kreuz ex Buin., *Mediolobivia* Backeb., *Pygmacolobivia* Backeb.], *Chamaecereus* Britt. & Rose (Buxbaum, 1957d), *Mila* Britt. & Rose.

Because of intermediate species, the delimitation of genera in this group is difficult and still unsatisfactory. This is true especially for the genus *Lobivia*, which therefore is considered here in its broadest sense.

#### SUBTRIBUS 3. **Borzicactinae** subtrib. nov.

*Echinocactae* K. Schum. p.p.; *Cereanae* Britt. & Rose, p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Trichocerei* Berg. nom. nud., p.p.; *Loxanthocerei* Backeb. nom. nud.; *Austroechinocacti* Backeb. nom. nud., p.p.; *Loxanthocerei* F. Buxb. nom. prov.; *Loxanthocereineae* F. Buxb. nom. prov.

Plantae columnares interdum brevicolumnares vel globosae; floribus elongato-infundibuliformibus vel tubiformibus (apud genus *Oroya* campanulatis); receptaculo petaloideo-colorato, squamoso et piloso rarissime subnudo vel nudo, saepe curvato itaque floribus pseudozygomorphis vel zygomorphis; perianthio haud permagno saepe reducto minuto atque minutissimo; camera nectarifera numquam presente. Genus typicum. *Borzicactus* Ricco.

Habit columnar or short-columnar (globular only in highly advanced, high montane genera, as in *Oroya*). Perianth relatively small or even much reduced; receptacle conspicuously colored, elongate-funnelform or tubular (campanulate only in *Oroya*), often more or less zygomorphic, nectar chamber very distinct (hummingbird flowers).

Genera (included for the present). *Loxanthocereus* Backeb. (including *Maritimocereus* Akers & Buin.), *Borzicactus* Ricco. (including *Bolivocereus* Card., ?*Clistanthocereus* Backeb.), *Denmoza* Britt. & Rose, *Cleistocactus* Lem. (Buxbaum 1956d), *Seticereus* Backeb., *Oreocereus* (Berg.) Ricco., *Morawetzia* Backeb., *Arequipa* Britt. & Rose, *Matucana* Britt. & Rose, *Oroya* Britt. & Rose.

#### TRIBUS VI. **Notocactae** trib. nov.

*Echinocactae* K. Schum. p.p. (1898, p. 46, Gruppe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Cactanae* Britt. & Rose (1922, p. 216, Subtribe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Erianthi* Berg. nom. nud., p.p. (1926, p. 68, 97, Sippe); *Gymnocerei* Berg. nom. nud., p.p. (as to "Cactoides");

1926, p. 55, 97, Sippe) ; *Austroechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 35, Natio) ; *Boreoechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 54, Natio) ; *Cephalocacti* Backeb. nom. nud. (1938, Sippe; 1942, p. 53, Natio) ; *Pseudotrichocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus) ; *Pseudotrichocereidinae* F. Buxb. nom. prov. (1956h, System 2, Tribus; here the tribe was further broken into the following provisional subtribes: *Notocactinae*, *Neoporteriinae*, *Parodiinae*, *Melocactinae*, *Gymnocalycinae*, and an unnamed subtribe).

Plantae simplices vel basi ramosae, globosae vel applanatae, rarius elongatae brevicolumnares, nonnumquam pusillimae, costatae vel costis divisis, tubercula sub areolis posita formantibus; floribus ex areola quaque unico vel pluribus, vel ex pseudocephalio vel ex cephalio terminali orientibus; receptaculo campanulato vel infundibuliformi; pericarpello et receptaculo squamosis (apud genus *Melocactus* receptaculo nudo petaloido), in axillis squamarum areoliferis vel rarius nudis; areolis pericarpelli et receptaculi valde pilosis rarissime lanatis spinosisque, superioribus plerumque setosis; staminibus supra sulcum nectariferum toto receptaculo usque ad faucem aequaliter insertis; foliis perianthii nonnumquam basi connatis; seminibus habitu variabilissimis typo testae verrucoso, variabili. Genus typicum. *Notocactus* (K. Schum.) Berger.

Stems simple or branching from base, globular to applanate, more rarely short-columnar, in the most advanced genera dwarfish; body ribbed, or the ribs divided into humps or even hump-like tubercles which occur below the areoles. Flowers solitary or several from the same areole, sometimes in a pseudocephalium or a terminal cephalium; pericarpel and receptacle covered with more or less numerous scales, the scales small, bearing in their axils much long wool, hairs, and, especially near the throat, stiff bent bristles or sometimes also fine bristle-like spines, sometimes (in *Gymnocalycium* and allies) the scales less numerous and naked in their axils, more rarely the flower areoles somewhat spiny or occasionally (in *Melocactus*) the flowers simplified to a "Mammillaria-shape", the petaloid receptacle lacking both scales and areoles; receptacle campanulate to funnelform, the tube sometimes elongate above margin of receptacle by union of basis of inner perianth segments, the stamens distributed equally from the distinct nectar furrow up to top of the receptacle. Seeds various in shape, the testa verrucose but the warts sometimes spine-like or secondarily flattened, the testa then smooth. South America (except *Astrophytum*).

Genera (included for present). *A. Eriosyce* Phil. *B. Austrocactus* Britt. & Rose, *Notocactus* (K. Schum.) Berg. (including *Brasilicactus* Backeb. and ?*Eriocactus* Backeb.), *Islaya* Backeb. *C. Parodia* Speg., *Frailea* Britt. & Rose, *Astrophytum* Lem. (Buxbaum, 1951e, 1951g), *Blossfeldia* Werd. *D. Malacocarpus* Salm-Dyck non Fisch. & Mey., *Melocactus* Link & Otto. *E. Neoporteria* Britt. & Rose [including *Neochilenia* Backeb. (invalid name.), *Horridocactus* Backeb., and *Pyrhocactus* Berg.], *Copiapoa* Britt. & Rose. *F. Gymnocalycium* Pfeiff. (according to personal communication from P. C. Hutchison in 1956, including

*Weingartia* Werd. and *Brachycalycium* Backeb.), *Neowerdermannia* Backeb., *Discocactus* Pfeiff.

In 1953 I first advanced a provisional grouping of genera for the Notoacteae, then called the Pseudotrilocereideae (Buxbaum, 1953a), and in 1956 (Buxbaum 1956h) I presented provisional subtribal names. My studies now indicate that these original groupings must be rearranged somewhat, but the research is not yet completed for final publication. For the present, I wish only to arrange the genera of the tribe into natural groups (A-F) as indicated in the preceding paragraph. The inclusion of *Neochilenia*, *Horridocactus*, and *Pyrrhocactus* under *Neoporteria* was first proposed in 1953 (Buxbaum, 1953a) and P. C. Hutchison (Verbal comm., 1956) has since confirmed the union of at least *Neochilenia* and *Horridocactus* with *Neoporteria*.

This tribe was confused by former authors with Berger's Trichocerei (Trilocereae of the present treatment). It is necessary to separate it because it clearly has had a separate evolution, possibly originating from *Corryocactus*-like ancestors. It is characterized by the acrotony of the receptacular areoles, the uppermost part of which are distinctly advanced, bearing more vigorous bristles than the lower ones, and by the arrangement of the stamens which differs distinctly from the arrangement in the Trilocereae.

#### TRIBUS VII. **Echinocereae** trib. nov.

*Echinocacteae* K. Schum. p.p. (1898, p. 46, Gruppe); *Cereanae* Britt. & Rose, p.p. (1920, p. 1, Subtribe); *Echinocereanae* Britt. & Rose, p.p. (1922, p. 3, Subtribe); *Nyctocerei* Berg. nom. nud., p.p. (1926, p. 45, 95, Sippe); *Echinocerei* Backeb. nom. nud. (1938, Sippe; 1942, p. 42, Natio); *Heliocerei* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 45, Natio); *Echinocereideae* F. Buxb. nom. prov. (1953a, p. 3, Tribus); *Echinocereidineae* F. Buxb. nom. prov. (1956h, System 2, Tribus).

Frutices parvi plerumque ramis ascendentibus cylindricis teneribus, rarissime magni columnares repentes, vel plantae succulentissimae brevicolumnares vel globosae, erectae vel prostratae; ramis costatis plerumque spinosissimis, spinis saepe tenui-acicularibus et densissime positis; floribus conspicuis, diurnis, coloratis; pericarpello, plerumque etiam receptaculo squamosis spinosissimis (genere *Rathbunia* excepto); floribus radiatis apud genus *Rathbunia* zygomorphis. Genus typicum. *Echinocereus* Engelm.

Plants usually short-columnar or globular, the stem erect or prostrate, or plants low, much branched, shrub-like, the branches sometimes thin and weak, or rarely plants large, prostrate; branches ribbed, densely spiny, the spines strong to weak. Flowers conspicuous, day-blooming, colored, radiate (in *Rathbunia* zygomorphic); pericarpel and usually even the receptacle bearing scales, those of the pericarpel smaller, those of the receptacle larger and elongate with very spiny axillary areoles (except in *Rathbunia*.) North America.

Genera. *Bergerocactus* Britt. & Rose, *Machaerocereus* Britt. & Rose, *Rathbunia* Britt. & Rose, *Wilcoxia* Britt. & Rose (including ?*Cullmannia* Dist.), *Echinocereus* Engelm.

The Echinocereae was first established by Britton and Rose as a subtribe (Echinocereanae). Besides *Echinocereus* they included in it *Lobivia* and its relatives, which are here assigned to Tribe Trichocereae, Subtribe Rebutinae. Berger did not recognize Britton and Rose's Echinocereanae, transferring the genera belonging in that group to form a day-blooming branch of his Nyctocerei. However, the connection with the Nyctocerei seems to be a very distant one, if it exists at all. Although much work still needs to be done on the Echinocereae, it seems to be well defined as presented here.

#### TRIBUS VIII. ECHINOACTEAE K. Schum. emend.

*Echinocactae* K. Schum. p.p. (1898, p. 46, Gruppe, = Tribus, p. 29); *Mamillariae* K. Schum. (1898, p. 472, Gruppe); *Echinocactanae* Britt. & Rose, p.p. (1922, p. 77, Subtribe); *Coryphanthanae* Britt. & Rose (1923, p. 3, Subtribe); *Erianthi* Berg. nom. nud., p.p. (1926, p. 68, 97, Sippe); *Lepidanthi* Berg. nom. nud. (1926, p. 70, 98, Sippe); *Gymnanthi* Berg. nom. nud. (1926, p. 74, 98, Sippe); *Pseudomamillariae* Berg. nom. nud. (1926, p. 80, 98, Sippe); *Chasmatothelae* Berg. nom. nud. (*ibid.*, Sippe); *Coryphanthae* Berg. nom. nud. (*ibid.*, Sippe); *Mamillariae* Berg. nom. nud. (*ibid.*, Sippe); *Cochemieae* Berg. nom. nud. (1926, p. 80, 99, Sippe); *Pelecyporae* Berg. nom. nud. (*ibid.*, Sippe); *Ariocarpi* Berg. nom. nud. (*ibid.*, Sippe); *Boreoechinocacti* Backeb. nom. nud., p.p. (1938, Sippe; 1942, p. 54, Natio); *Euechinocactineae* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 98; 1951h, p. 31; 1953a, p. 3: Tribus); *Euechinocactidineae* F. Buxb. nom. prov. (1956h, System 4, Tribus); *Echinocacti* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7: Linea); *Euechinocactineae* F. Buxb. nom. prov. (1956h, System 4, Subtribe); *Ramus* or *Ramis* [sic!] I F. Buxb. nom. prov. 1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Thelocactineae* F. Buxb. nom. prov. (1956h, System 4, Subtribus); *Thelocacti* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Strombocacti* F. Buxb. nom. nud. (1951b, p. 193, 197; 1951c, p. 100; 1951h, p. 33; 1953a, p. 7; 1956h, System 4; cf. also Buxbaum 1936, 1937: Linea); *Ramus* or *Ramis* [sic!] II F. Buxb. nom. prov. (1951b, p. 193, 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Ferocactineae* F. Buxb. nom. prov. 1956h, System 4, Subtribus); *Ferocacti* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Neobesseya* F. Buxb. nom. nud. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7; 1956h, System 4: Linea); *Ramus* or *Ramis* [sic!] III F. Buxb. nom. prov. (1951b, p. 197; 1951c, p. 99; 1951h, p. 33; 1953a, p. 7); *Coryphanthae* F. Buxb. nom. nud. (1951b, p. 197, Linea); *Coryphanthineae* F. Buxb. nom. prov. (1956h, System 4, Subtribe).

Cactaceae giganteae usque ad pusillae, brevicolumnares vel globosae vel depressae, costatae vel tuberculatae; tuberculis habitu variabili nonnumquam folioideis; areolis generum tuberculatorum plus deductorum vel in sulcam elongatum vel in areolam spinigeram et axillam florigeram divisis; areolis generum costatorum saepe glanduliferis; floribus ex margine superiore areolarum vel ex sulco tuberculi vel ex axillis orientibus, radiatis, rarissime zygomorphis (genus *Cochemiea*), diurnis; pericarpello crasso squamosissimo lanuginosissimo, receptaculo fere absente, vel floribus plus minusve campanulatis, receptaculo valde squamoso, areolis in flore absentibus vel apud genera deductissima pericarpello nudo et receptaculo petaloideo; fructo plus minusve carnosio saepe uveriformi; seminibus funiculo brevi simplici adnatis in quattuor lineis differentibus: 1)



testa dura nigra, levi, perispermio conspicuo (subtribus Echinocactinae), 2) testa verrucosa vel tuberculis testae secundariter laevis itaque foveolis interstitialibus punctata sublevi, perispermio praesente vel reducto etiam abortu (subtribus Thelocactinae), 3) testa foveolata vel reticulata nigra vel brunea, perispermio praesente apud genera deducta reducto atque abortu (subtribus Ferocactinae), 4) testa levi, brunea, celulis minimis perispermio praesente (subtribus Coryphanthinae); blastis succulentissimis cotyledonibus triangularibus apud genera deductissima maxime reductis. Genus typicum. *Echinocactus* Link & Otto.

Plants short-columnar, globular, or depressed, gigantic to small or dwarfish; stems ribbed or bearing short-conic to finger-like or leaf-like tubercles; areoles borne on the ribs or at or near the top of each tubercle or sometimes elongate and forming a groove on the upper surface of the tubercle, in the most advanced genera serially divided into a spine-bearing areole at the apex of the tubercle and a flower-bearing (floriferous) and sometimes shoot-bearing areole in the axil, in primitive genera sometimes with glandular spines. Flowers borne at the upper margin of areole or from the groove or in the axil, radiate or rarely zygomorphic, day-blooming; pericarpel scaly and woolly, the receptacle almost absent in the most primitive genera, more or less elongated-campanulate and distinctly scaly in the more advanced genera, and petaloid in the most advanced genera. Fruit more or less fleshy to juicy. Seeds on short and simple funicles which vary greatly in the different lines of evolution: 1) testa smooth, hard, black, the perisperm conspicuous (Echinocactinae, the most primitive subtribe); 2) testa verrucose, mostly black, the perisperm present or absent, the warts of the testa in most advanced genera becoming secondarily smooth but with more or less distinct spots between the testa cells, i.e., "spotted testa" (subtribe Thelocactinae); 3) testa "pitted" or reticulate, i.e., the testa with outer cell walls sunken in, the perisperm present or absent (subtribe Ferocactinae); 4) testa smooth, brown, with very small scales, the perisperm present (subtribe Coryphanthinae). Seedlings succulent, the cotyledons small, triangular, finally reduced to small humps. North America, to Venezuela in South America.

This tribe contains all the North American short-columnar or globular cacti with spineless flowers except *Astrophytum* (Buxbaum, 1951e, 1951g). It is a very clear-cut phylogenetic unit which has been thoroughly studied and is well understood except as to less important details in its phylogeny. The most primitive subtribe is the Echinocactinae.

#### SUBTRIBUS 1. ECHINOCACTINAE Britt. & Rose emend.

*Echinocacteae* K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Erianthi* Berg. nom. nud., p.p.; *Boreoechinocacti* Backeb. nom. nud., p.p.; *Echinocacti* F. Buxb. nom. nud.; *Euechinocactineae* F. Buxb. nom. prov.

Echinocacteae giganteae brevicolumnares vel magnae globosae vel applanatae, costatae, spinosissimae; floribus pericarpello crasso squamosis-

simo pilosissimo (apud genus *Homalocephalam* parte inferiore nudo) seminibus magnis, testa nigra levi, rarius verrucosa vel minutissime reticulata, perispermio magno; embryonis cotyledonibus conspicuis triangularibus. Genus typicum. *Echinocactus* Link & Otto.

Plants short-columnar and gigantic to globular or applanate and conspicuous, ribbed, strongly spined. Flowers with the pericarpel thick, the scales numerous, with hairs and wool in their axils or (in *Homalocephala*) only at upper part; receptacle greatly reduced to almost absent. Seeds large; testa black, smooth or occasionally verrucose or somewhat reticulate; perisperm conspicuous. Embryo with cotyledons distinct, triangular.

Genera. *Echinocactus* Link & Otto, *Homalocephala* Britt. & Rose (possibly part of *Echinocactus*?)

#### SUBTRIBUS 2. **Thelocactinae** subtrib. nov.

*Echinocactae* K. Schum. p.p.; *Mamillariae* K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Lepidanthi* Berg. nom. nud., p.p.; *Gymnanthi* Berg. nom. nud.; *Pseudomamillariae* Berg. nom. nud., p.p.; *Chasmatothelae* Berg. nom. nud.; *Pelecyphorae* Berg. nom. nud.; *Ariocarpi* Berg. nom. nud.; *Boreoechinocacti* Backeb. nom. nud., p.p.; *Ramus* or *Ramis* [sic!] F. Buxb. nom. prov.; *Thelocactinae* F. Buxb. nom. prov.

*Echinocactae* parvae vel costatae costis saepe in tubercula divisus, vel tuberculatae; tuberculis nonnumquam folioideis, floribus receptaculo et pericarpello variabilibus, squamosis vel esquamosis, areolis absentibus; seminibus verrucosis, apud species nonnullas deductissimas secundariter levibus, foveolis interstitialibus punctatis; perispermio praesente vel absente. Genus typicum. *Thelocactus* (K. Schum.) Britt. & Rose.

Plants small, the ribs often divided into tubercles or humps, or the whole plant tuberculate, the tubercles sometimes leaf-like. Flowers very variable in shape; scales of the pericarpel and receptacle, when present, mostly without areoles in the axils (occasional exceptions). Seeds black; testa verrucose, the warts in the most advanced genera becoming secondarily smooth (applanate) but with more or less distinct spots between the testa cells, i.e., "spotted testa"; perisperm present or absent.

#### LINEA A. **Thelocacti** linea nov.

*Thelocacti* F. Buxb. nom. nud.

Plantae parvae globulares vel elongatae, costatae, costis in tubercula divisus vel tuberculatae; tuberculorum areolae apud genera deductissima in areolam spiniferam et axillam floriferam divisus; tuberculis nonnumquam sulcatis umquam folioideis; floribus prope apicem, vel ex margine superiore areolarum vel ex sulco vel ex axilla orientibus. Genus typicum. *Thelocactus* (K. Schum.) Britt. & Rose.

Plants small, globular or elongated, the ribs divided into tubercles or the plant tuberculate, finally reaching the "*Mammillaria* stage" with dimorphic areoles, the tubercles never leaf-like; spines strong, well-developed, sometimes hooked. Flowers borne near apex from the upper margin

of areoles or from the tubercle groove, or in the most advanced genera from the axils.

Genera (arranged in three natural groups). *A. Sclerocactus* Britt. & Rose, *Pediocactus* Britt. & Rose, *Utahia* Britt. & Rose. *B. Ancistrocactus* (K. Schum.) Britt. & Rose, *Hamatocactus* Britt. & Rose, cf. Buxbaum, 1951f (including *Glandulicactus* Backeb.), *Oehmea* F. Buxb. (Buxbaum 1951d), *Cumarinia* (Knuth) F. Buxb. *C. Echinomastus* Britt. & Rose, *Thelocactus* (K. Schum.) Britt. & Rose, *Neolloydia* Britt. & Rose, cf. Buxbaum, 1951d (including *Gymnocactus* Backeb.), *Rapicactus* F. Buxb. & Oehme, *Mammilloidya* F. Buxb. (Buxbaum 1951c. p. 64; 1951d).

#### LINEA B. *Strombocacti* linea nov.

*Strombocacti* F. Buxb. nom. nud.

Plantae parvae globosae, elongatae vel applanatae rarissime costatae costis applanatis plerumque tuberculatis tuberculis saepe folioides; spinis plerumque reductis nonnumquam papyrosis, saepe caduceis; floribus prope apicem ex margine areolarum vel ex sulco tuberculi vel ex axilla orientibus. Genus typicum. *Strombocactus* Britt. & Rose emend. F. Buxb.

Plants small, usually more or less globular, sometimes elongated, rarely with flattened and more or less divided (*Lophophora*, *Toumeyia* p.p.) ribs, or more frequently tuberculate with the tendency to develop leaf-like tubercles; spines mostly reduced, sometimes papery, sometimes nearly lacking. Flowers near apex, from the top, groove, or axil of the tubercles.

Genera (arranged in closely related groups). *A. Toumeyia* Britt. & Rose emend W. T. Marsh. [including *Turbinicarpus* (Backeb.) F. Buxb. & Backeb. and *Navajoa* Croiz.; according to W. Taylor Marshall (1947) and H. Bravo-H. and W. T. Marshall (1956, 1957) *Turbinicarpus* and *Navajoa* should be united with *Toumeyia*], *Lophophora* Coult. *B. Strombocactus* Britt. & Rose emend. F. Buxb., *Aztekium* Boed. *C. Leuchtenbergia* Hook., *Obregonia* Frič & Berg., *Encephalocarpus* Berg., *Ariocarpus* Scheidw. (including *Roseocactus* Berg.), *Neogomesia* Castañ. *D. Epithelantha* Web. ex Britt. & Rose, *Pelecyphora* Ehrenb.

#### SUBTRIBUS 3. *Ferocactinae* subtrib. nov.

*Echinocacteae* K. Schum. p.p.; *Mamillariaeae* K. Schum. p.p.; *Echinocactanae* Britt. & Rose, p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Lepidanthi* Berg. nom. nud., p.p.; *Pseudomamillariaeae* Berg. nom. nud., p.p.; *Coryphanthae* Berg. nom. nud., p.p.; *Mamillariae* Berg. nom. nud., p.p.; *Cochemieae* Berg. nom. nud.; *Ramus* or *Ramis* [sic!] II F. Buxb. Nom. prov.; *Ferocactinae* F. Buxb. nom. prov.

*Echinocacteae* magnitudine variantes a plantis maximis brevicolumnariis usque ad pygmaeis globularibus vel applanatis vel elongatis, costatis (costis apud genus *Echinofossulocactus* permultis lamellosis) vel tuberculatis; areolis generum tuberculorum ovatis vel in sulcam elongatis vel in areolam spiniferam et axillam floriferam divis; floribus squamosis vel nudis, pericarpello interdum petaloideo, fructibus carnoso-siccis vel uiformibus; seminibus foveolatis vel reticulatis, nigris vel bruneis, peri-

spermio praesente apud genera deductissima absente. Genus typicum. *Ferocactus* Britt. & Rose.

Plants short-columnar and large to globular or elongated and very small, ribbed in primitive genera, the ribs strong (*Ferocactus*) or thin and numerous (*Echinofossulocactus*), tuberculate in advanced genera; areoles in tuberculate plants elongate or dimorphic. Flowers scaly to naked, if naked, then the receptacle petaloid. Fruit dry-fleshy or juicy. Seeds black or in the most advanced species brown; testa cells with the outer cell walls sunken to produce a "pitted" testa, or if cells larger, the testa reticulate; perisperm present in the more primitive genera, absent in the more advanced genera.

#### LINEA A. *Ferocacti* linea nov.

*Ferocacti* F. Buxb. nom. nud.

Plantae magnae, vel brevicolumnares vel globosae vel depresso-globosae, costatae (genera *Coloradoa* excepto), floribus ex margine areolarum orientibus, pericarpello et receptaculo squamoso. Genus typicum. *Ferocactus* Britt. & Rose.

Plants large, short-columnar to depressed-globose, ribbed or (in *Coloradoa*) tuberculate. Flowers borne at the margins of areoles; pericarpel and receptacle scaly.

Genera. *Ferocactus* Britt. & Rose (including *Brittonia* Houghton ex Armstr., invalid name), *Echinofossulocactus* Lawr., *Coloradoa* Boissiev. & C. Davids.

#### LINEA B. *Neobesseyae* linea nov.

*Neobesseyae* F. Buxb. nom. nud.

Plantae parvae vel pusillae, vel elongatae vel globosae vel depresso-globosae, rarissime brevicolumnares; areolis in sulcum extensis vel in areolam spiniferam et axillam floriferam divis; floribus ex sulco vel ex axilla orientibus, receptaculo plus minusve petaloideo, squamoso vel nudo. Genus typicum. *Neobesseyea* Britt. & Rose.

Plants small to dwarfish, elongate to depressed-globular, especially in some genera short-columnar in age, tuberculate; areoles elongate or dimorphic. Flowers borne from the groove or axil; receptacle more or less petaloid, scaly in the less advanced genera, naked in the highly advanced genera.

Genera. *Escobaria* Britt. & Rose emend. F. Buxb., 1951d, p. 78 (including *Escobesseyea* Hester, invalid name), *Leptocladodia* F. Buxb. (Buxbaum, 1954c = *Leptocladia* F. Buxb. 1951 non Agardh, 1892, *Mamilloopsis* (Morren) Britt. & Rose, *Neobesseyea* Britt. & Rose (Buxbaum, 1951d), *Dolichothele* (K. Schum.) Britt. & Rose emend. Werderm. & F. Buxb. (Buxbaum, 1956g), *Pseudomammillaria* F. Buxb. (Buxbaum 1951c, p. 84; 1951d), *Mammillaria* Haw. non Stackh. [including *Bartschella* Britt. & Rose (Buxbaum, 1954d), *Chilita* Orcutt emend. F. Buxb. (1954b), *Ebnerella* F. Buxb., *Krainzia* Backeb., *Phellosperma* Britt. & Rose, *Porfuria* Boed., *Solisia* Britt. & Rose], *Cochemia* (K. Brand.) Walt.

The seed of *Mammillaria simplex* Haw., type species of the genus, was not available to me for many years. According to the description it seemed to belong to the same type as the perisperm-containing *Mammillaria* seeds, and therefore the genus was placed in the Subtribe Coryphanthinae (Buxbaum 1950, 1951c, 1951h). Now the seed is recognized to have a pitted testa, indicating that the genus *Mammillaria* Haw. must be transferred to the Neobesseyae (Buxbaum, 1956a). This makes it possible to reunite again several of the separated genera with *Mammillaria*, as has been suggested as perhaps more desirable by Moran (1954). Nevertheless, some species of the genus, as presently conceived, must still be retained in the Coryphanthinae as they have the smooth testa and distinct perisperm of that subtribe, but research on this problem is not yet finished. Thus the genus *Mammillaria*, as herein circumscribed, is not homogeneous.

#### SUBTRIBUS 4. CORYPHANTHINAE Britt. & Rose emend.

*Mamillarieae* K. Schum. p.p.; *Coryphanthanae* Britt. & Rose, p.p.; *Coryphanthae* Berg. nom. nud., p.p.; *Ramus* or *Ramis* [sic!] III F. Buxb. nom. Prov.; *Coryphanthae* F. Buxb. nom. nud.; *Coryphanthineae* F. Buxb. nom. prov.

Plantae magnitudinae media rarius parvae globosae, adultissimae interdum brevicolumnares, tuberculatae, areolis aut in sulcum tuberculi extensis aut in areolam spiniferam et axillam floriferam divisas, saepe glanduligeris; floribus ex sulco tuberculi vel ex axilla orientibus, squamosis vel nudis; receptaculo plus minusve petaloideo; seminibus levibus, bruneis, neque foveolatis neque verrucosis, interdum rugosis, testae cellulis minutissimis; perispermio semper praesente magno vel distincto. Genus typicum. *Coryphantha* (Engelm.). Lem. sensu F. Buxb. (1951c. p. 96-97).

Plants medium-sized to small, globular to short-columnar, tuberculate; areoles extended to a groove or dimorphic. Flowers borne in the groove or axil. Seeds brown; testa smooth with very small cells, neither pitted nor spotted, sometimes shriveling; perisperm large or at least distinct.

Genus. *Coryphantha* (Engelm.) Lem. sensu F. Buxb.

At present this subtribe contains only the genus *Coryphantha* modified to include *Lepidocoryphantha* Backeb. (Buxbaum, 1951b, 1951c, 1956c). After further research the present species of *Mammillaria* which have a smooth testa and distinct perisperm undoubtedly will be transferred to the Coryphanthinae under a new generic name.

#### SUMMARY OF THE PHYLOGENETIC DIVISION OF THE CEREIOIDEAE

##### TRIBUS I. LEPTOCEREAE F. Buxb.\*<sup>3</sup>

Armatocereus Backeb.

Corryocactus Britt. & Rose

Erdisia Britt. & Rose

Eulychnia Phil. (incl. Philippicereus Backeb.)

Facheiroa Britt. & Rose (incl. ?Thrixanthocereus Backeb.,  
?Vatricania Backeb.)

Leocereus Britt. & Rose

<sup>3</sup>An asterisk marks each new name, each name in new status, and the name of each taxon whose circumscription is emended.

Leptocereus (Berg.) Britt. & Rose  
 Neoraimondia Britt. & Rose (incl. Neocardenasia Backeb.)  
 Neoabbottia Britt. & Rose  
 Samaipaticereus Card.  
 Zehntnerella Britt. & Rose

TRIBUS II. HYLOCEREAE F. Buxb.\*

SUBTRIBUS 1. NYCTOCEREINAE F. Buxb.\*

LINEA A. NYCTOCEREI F. Buxb.\*

Nyctocereus (Berg.) Britt. & Rose  
 Brachycereus Britt. & Rose  
 Peniocereus (Berg.) Britt. & Rose

LINEA B. ACANTHOCEREI F. Buxb.\*

Acanthocereus (Berg.) Britt. & Rose  
 Dendrocereus Britt. & Rose

LINEA C. HARRISIAE F. Buxb.\*

Harrisia Britt.  
 Eriocereus (Berg.) Ricco.

LINEA D. HELIOCEREI F. Buxb.\*

Heliocereus (Berg.) Britt. & Rose  
 Aporocactus Lem.

SUBTRIBUS 2. HYLOCEREINAE Britt. & Rose emend. F. Buxb.\*

A. Selenicereus (Berg.) Britt. & Rose

Cryptocereus Alex.  
 Deamia Britt. & Rose  
 Strophocactus Britt. & Rose

B. Mediocactus Britt. & Rose

Wilmattea Britt. & Rose  
 Hylocereus (Berg.) Britt. & Rose

C. Werckleocereus Britt. & Rose

Weberocereus Britt. & Rose  
 Eccremocactus Britt. & Rose

SUBTRIBUS 3. EPIPHYLLINAE Britt. & Rose emend. F. Buxb.\*

Epiphyllum Haw. (incl. Marniera Backeb.)

SUBTRIBUS 4. DISOACTINAE F. Buxb.\*

Nopalxochia Britt. & Rose  
 Lobeira Alex.  
 Bonifazia Standl. & Steyerm.  
 Chiapasia Britt. & Rose  
 Disocactus Lindl.  
 Pseudorhipsalis Britt. & Rose  
 Wittia K. Schum.

SUBTRIBUS 5. RHIPSALINAE Britt. & Rose emend. F. Buxb.\*

LINEA A. PFEIFFERAE F. Buxb.\*

Pfeiffera Salm-Dyck  
 Acanthorhipsalis (K. Schum.) Britt. & Rose

LINEA B. SCHLUMBERGERAE F. Buxb.\*

Erythrorhipsalis Berg.  
 Hatiora Britt. & Rose (incl. Pseudozygocactus Backeb.)

Rhipsalidopsis Britt. & Rose (incl. Epiphyllopsis Berg., invalid name)  
 Schlumbergera Lem.  
 Zygocactus K. Schum. (incl. Epiphyllanthus Berg.)

LINEA C. RHIPSALES F. Buxb.\*  
 Rhipsalis Gaertn.  
 Lepismium Pfeiff.

TRIBUS III. PACHYCERAE F. Buxb.\*

Pachycereus (Berg.) Britt. & Rose  
 Lemaireocereus Britt. & Rose sensu lat. [incl. Hertrichocereus Backeb., Isolatocereus (Backeb.) Backeb., Marginatocereus (Backeb.) Backeb., Neolemaireocereus Backeb. (invalid name), Polaskia Backeb., Ritterocereus Backeb., Stenocereus (Berg.) Ricco.]  
 Neobuxbaumia Backeb. emend. Dawson & F. Buxb.  
 Carnegiea Britt. & Rose non Perkins  
 Mitrocereus (Backeb.) Backeb. (incl. Backebergia Bravo H.)  
 Cephalocereus Pfeiff. [incl. Haseltonia Backeb., Pilosocereus Byles & Rowley (= Pilocereus K. Schum. non Lem.) p.p.]  
*Genera incertae sedis:*  
 Escontria Rose  
 Anisocereus Backeb.

TRIBUS IV. CEREAE Britt. & Rose emend. F. Buxb.\*

Arrojadoa Britt. & Rose non Mattf.  
 Austrocephalocereus (Backeb.) Backeb. (incl. Coleocephalocereus Backeb.)  
 Browningia Britt. & Rose (?incl. Gymnanthocereus Backeb.)  
 Cereus Mill. (incl. Monvillea Britt. & Rose, Brasilicereus Backeb., Subpilocereus Backeb.)  
 Jasminocereus Britt. & Rose  
 Stephanocereus Berg.  
 Stetsonia Britt. & Rose  
*Genera incertae sedis:*  
 Lophocereus (Berg.) Britt. & Rose  
 Myrtillocactus Cons.

TRIBUS V. TRICHOCERAE F. Buxb.\*

SUBTRIBUS 1. TRICHOCEREINAE F. Buxb.\*

Trichocereus (Berg.) Ricco. (incl. Helianthocereus Backeb., Leucostele Backeb., Roseocereus Backeb., Weberbauerocereus Backeb.)  
 Echinopsis Zucc. [incl. Pseudolobivia (Backeb.) Backeb.]  
 Haageocereus Backeb. (incl. Neobinghamia Backeb., Peruvo-cereus Akers)  
 Arthrocerus Berg. [incl. Setiechinopsis (Backeb.) de Hass]  
 Espostoa Britt. & Rose (incl. Pseudoespostoa Backeb.)  
 Soehrensia Backeb.  
 Acanthocalycium Backeb.

SUBTRIBUS 2. REBUTINAE Donald emend. F. Buxb.\*

Lobivia Britt. & Rose sensu lat. (incl. Acantholobivia Backeb., Hymenorebutia Frič ex Buin., Sulcorebutia Backeb.)  
 Rebutia K. Schum. [incl. Aylosteria Speg., Cylindrorebutia Frič]

& Kreuz (invalid name), *Digitorebutia* Frič & Kreuz ex Buin., *Mediolobivia* Backeb., *Pygmaeolobivia* Backeb.]  
*Chamaecereus* Britt. & Rose  
*Mila* Britt. & Rose

SUBTRIBUS 3. BORZICACTINAE F. Buxb.\*

*Loxanthocereus* Backeb. (incl. *Maritimocereus* Akers & Buin.)  
*Borzicactus* Ricco. (incl. *Bolivocereus* Card., ?*Clistanthocereus* Backeb.)  
*Denmoza* Britt. & Rose  
*Cleistocactus* Lem.  
*Seticereus* Backeb.  
*Oreocereus* (Berg.) Ricco.  
*Morawetzia* Backeb.  
*Arequipa* Britt. & Rose  
*Matucana* Britt. & Rose  
*Oroya* Britt. & Rose

TRIBUS VI. NOTOCACTEAE F. Buxb.\*

- A. *Eriosyce* Phil.
- B. *Austrocactus* Britt. & Rose  
*Notocactus* (K. Schum.) Berg. (incl. *Brasilicactus* Backeb., ?*Eriocactus* Backeb.)  
*Islaya* Backeb.
- C. *Parodia* Speg.  
*Frailea* Britt. & Rose  
*Astrophytum* Lem.  
*Blossfeldia* Werd.
- D. *Malacocarpus* Salm-Dyck non Fisch. & Mey.  
*Melocactus* Link & Otto
- E. *Neoporteria* Britt. & Rose [incl. *Neochilenia* Backeb. (invalid name), *Horridocactus* Backeb., *Pyrrhocactus* Berg.]  
*Copiapoa* Britt. & Rose
- F. *Gymnocalycium* Pfeiff. (incl. *Brachycalycium* Backeb., *Weingartia* Werd.)  
*Neowerdermannia* Backeb.  
*Discocactus* Pfeiff.

TRIBUS VII. ECHINOCEREAE (Britt. & Rose) F. Buxb.\*

*Bergerocactus* Britt. & Rose  
*Machaerocereus* Britt. & Rose  
*Rathbunia* Britt. & Rose  
*Wilcoxia* Britt. & Rose  
*Echinocereus* Engelm.

TRIBUS VIII. ECHINOCACTEAE K. Schum. emend. F. Buxb.\*

SUBTRIBUS 1. ECHINOCACTINAE Britt. & Rose emend. F. Buxb.\*

*Echinocactus* Link & Otto  
*Homalocephala* Britt. & Rose

SUBTRIBUS 2. THELOCACTINAE F. Buxb.\*

LINEA A. THELOCACTI F. Buxb.\*



- A. *Sclerocactus* Britt. & Rose  
*Pediocactus* Britt. & Rose  
*Utahia* Britt. & Rose
- B. *Ancistrocactus* (K. Schum.) Britt. & Rose  
*Hamatocactus* Britt. & Rose (incl. *Glandulicactus* Backeb.)  
*Oehmea* F. Buxb.  
*Cumarinia* (Knuth) F. Buxb.
- C. *Echinomastus* Britt. & Rose  
*Thelocactus* (K. Schum.) Britt. & Rose  
*Neolloydia* Britt. & Rose (incl. *Gymnocactus* Backeb.)  
*Rapicactus* F. Buxb. & Oehme  
*Mammilloidia* F. Buxb.

LINEA B. STROMBOCACTI F. Buxb.\*

- A. *Toumeyia* Britt. & Rose emend. W. T. Marshall [incl. *Turbini-*  
*carpus* (Backeb.) F. Buxb. & Backeb. and *Navajoa* Croiz.]  
*Lophophora* Coult.
- B. *Strombocactus* Britt. & Rose emend. F. Buxb.  
*Aztekium* Boed.
- C. *Leuchtenbergia* Hook.  
*Obregonia* Frič & Berg.  
*Encephalocarpus* Berg.  
*Ariocarpus* Scheidw. (incl. *Roseocactus* Berg.)  
*Neogomesia* Castañ.
- D. *Epithelantha* Web. ex. Britt. & Rose  
*Pelecyphora* Ehrenb.

SUBTRIBUS 3. FEROCACTINAE F. Buxb.\*

LINEA A. FEROCACTI F. Buxb.\*

- Ferocactus* Britt. & Rose (incl. *Brittonia* Houghton ex Armstr.,  
invalid name)  
*Echinofossulocactus* Lawr.  
*Coloradoa* Boissév. & C. Davids.

LINEA B. NEOBESSEYAE F. Buxb.\*

- Escobaria* Britt. & Rose emend. F. Buxb. (incl. *Escobeseya*  
Hester, invalid name)  
*Leptocladodia* F. Buxb.  
*Mamilloopsis* (Morren) Britt. & Rose.  
*Neobeseya* Britt. & Rose  
*Dolichothele* (K. Schum.) Britt. & Rose emend. Werderm. &  
F. Buxb.  
*Pseudomammillaria* F. Buxb.  
*Mammillaria* Haw. non Stackh. (incl. *Bartschella* Britt. &  
Rose, *Chilita* Orcutt emend. F. Buxb., *Ebnerella* F. Buxb.,  
*Krainzia* Backeb., *Phellosperma* Britt. & Rose, *Porfiria*  
Boed., *Solisia* Britt. & Rose)  
*Cochemiea* (K. Brand.) Walt.

SUBTRIBUS 4. CORYPHANTHINAE Britt. & Rose emend. F. Buxb.\*

- Coryphantha* (Engelm.) Lem. (incl. *Lepidocoryphantha*  
Backeb.)

## CEREOIDEAE INCERTAE SEDIS:

Azureocereus Akers & Johns.  
 Castellanosia Card.  
 Micranthocereus Backeb.  
 Neodawsonia Backeb.

University of Graz  
 Austria

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## MOSSES OF CALIFORNIA VI. HALL NATURAL AREA AND MONO COUNTY

LEO FRANCIS KOCH

On the eastern slope of the Sierra Nevada, about five miles north of Tioga Pass and bordering Yosemite National Park, California, is the Harvey Monroe Hall Natural Area, the scene of the historic transplant experiments initiated by Dr. Hall and continued by J. Clausen, D. D. Keck, and W. M. Hiesey under the auspices of the Carnegie Institution of Washington. During the last decade, the writer has studied the collections of mosses made in this area by Dr. D. G. Catcheside in 1947 and by Dr. E. H. Ketchledge in 1953. I am indebted to Dr. Catcheside for placing his collection at my disposal, and to Dr. W. M. Hiesey for the loan of Dr. Ketchledge's collections. Dr. Malcolm A. Nobs of the Carnegie Institution at Stanford has been especially helpful in providing general information about the Natural Area and details of its topography and flora. Both Dr. Catcheside and Dr. Ketchledge kindly provided additional information and data about their collections.

The Harvey Monroe Hall Natural Area is part of the Toiyabe National Forest and includes approximately nine square miles, of which Mount Conness is the highest point at 12,556 feet above sea level. The area is severely glaciated and dissected by three hanging valleys which radiate in an easterly direction from the Sierran crest. The floors of these valleys are typically U-shaped, and alternate between alpine meadows and dry terminal moraines. According to Dr. Nobs, the habitats there are diverse, ranging from alpine bogs to places which are nearly desert-like and inhabited by sage-brush. *Pinus murrayana* Balf. and *P. albicaulis* Engelm. are dominant, the first at lower altitudes and on slopes with a southern exposure, and the second at higher altitudes and on slopes with northern exposure. Tree line is about 11,500 feet above sea level, and the alpine turf above it includes the caespitose *Salix petrophila* Rydb. as well as many "cushion plants." From the information available at the Carnegie Institution at Stanford, the vascular plants of the area include more than 330 species, of which 10 are pteridophytes and 6 are gymnosperms.

In this area, Dr. Catcheside and Dr. Ketchledge collected a total of 58 species of mosses, of which 5 appear to be the first authentic records from California: *Blindia acuta*, *Bryum muehlenbeckii*, *B. pallens*, *Campylium stellatum*, and *Mnium orthorrhynchum*. Dr. Howard A. Crum identified

one of the specimens as *Ceratodon purpureus* var. *dimorphus*, another addition to the known moss taxa of California. The specimens of *Bryum* and *Mnium* were named by Dr. A. L. Andrews, and Dr. H. S. Conard verified the identity of *Campylium stellatum*.

The earliest collections of mosses known to me from Mono County are of *Cratoneuron filicinum* and *Oncophorus virens*. These were collected by H. N. Bolander between 1860 and 1864 when he was associated with the California State Geological Survey, and are probably the specimens reported from Mono Pass by Leo Lesquereux (1868). Most later collections in Mono County, other than those of Catcheside and Ketchledge, were obtained from Leevining Grade below Tioga Pass, where the author found specimens representing 17 taxa in 1947.

As a unit, these collections are especially interesting because, in addition to being the only ones known from the Hall Natural Area, they are the first adequate sample of the moss flora of the eastern escarpment of the Sierra Nevada in California. When these species are classified according to their world-wide distribution in my previously published system (Koch, 1954, p. 522), the data are as follows:

Distributional division	Number of species		Percentage of species	
	California	Mono Co.	California	Mono Co.
A. Represented in both hemispheres of the earth:				
1. Weedy	3	none	0.9	none
2. Cold to temperate	56	22	17.7	30.6
3. Temperate to subtropical	17	4	5.4	5.5
B. Restricted to the northern hemisphere:				
4. Anomalous	4	none	1.3	none
5. Three Boreal Continents	100	27	31.7	37.5
6. Europe-North America	39	8	12.3	11.1
7. Asia-North America	5	none	1.6	none
8. Restricted to North America	93	11	29.3	15.3
Totals	317	72	100.2	100.0

The data show a significantly lower percentage of mosses known from Mono County, when compared to the entire state of California, whose distribution is limited to North America; contrariwise, there is a significantly higher percentage of Mono County mosses whose distribution extends from colder to temperate regions in both hemispheres and into all three of the boreal continents, but not into the austral hemisphere. Only two of the mosses known from Mono County are endemic to California, which is less than half of the percentage of mosses endemic to California in its entirety. Also of interest is the absence of all representatives of the Asia-North America division from the Mono County flora.

In the following catalogue of the species of mosses known to be part of the flora of Mono County, California, the names of Catcheside and Ketchledge are abbreviated to C. and K., respectively. The specimens collected

by Dr. Catcheside are represented in his personal herbarium at the University of Birmingham, and duplicates of many of them are in the Herbarium of the University of Michigan or of the author. All of Dr. Ketchledge's collections are represented in the Herbarium of the Carnegie Institution of Washington at Stanford, California.

#### DITRICHACEAE

CERATODON PURPUREUS (H.) Brid. *K.* 1993; var. DIMORPHUS (Phil.) C. Jens. *C.* 4774. The varietal form is diminutive and grows in minute cushions which at first glance do not resemble typical specimens of the species. According to Dr. H. A. Crum, who identified this specimen, the variety has also been found in North America by Macoun at Lake Agnes above Lake Louise in Alberta, Canada, although not mentioned by Grout (1928-40).

DISTICHUM CAPILLACEUM (H.) B. S. G. *K.* 1918; *Koch* 1780i (UM), Leevining.

#### SELIGERACEAE

BLINDIA ACUTA (H.) B. S. G. *K.* 1935, 1984.

#### DICRANACEAE

ONCOPHORUS VIRENS Brid. *Bolander* (NY), Mono Pass (Lesq. 1868); *C.* 4790, 4797; *K.* 1904, 1981.

#### POTTIACEAE

DESMATODON LATIFOLIUS var. MUTICUS Brid. *C.* 4784, 4786; *K.* 1907, 1927, 1946.

TORTULA PRINCEPS de Not. *C.* 4756.

WEISSIA CONTROVERSA H. *K.* 1911, 1912.

#### GRIMMIACEAE

GRIMMIA AGASSIZII (Sull.) Lesq. & James. *C.* 47105, fide Sayre.

G. ANODON B. S. G. *Alexander* (UC 719364), Hot Spring formation 2 miles southeast of Bridgeport.

G. BREVIROSTRIS Will. *C.* 4783.

G. HAMULOSA Lesq. *C.* 47143, 47144, 47145.

G. MONTANA B. S. G. *C.* 4782.

RHACOMITRIUM HETEROSTICHUM (H.) Brid. *C.* 47146; *K.* 1939.

SCOULERIA AQUATICA Hook. *Koch* 1769 (UM), Leevining.

#### BRYACEAE

BRYUM ALPINUM With. *C.* 47101.

B. ANGUSTIRETE Kindb. *Hall.* (CAS 221858), Leevining; *C.* 47148.

B. FLAGELLOSUM Kindb. *C.* 47129; *Koch* 1773 (UM), Leevining.

B. MUEHLENBECKII B. S. G. *C.* 4775, on wet rocks above cabin, altitude 10,200 feet. Previously reported by Andrews (1940) "from the northern United States (Maine, New Hampshire, northern Michigan, Idaho) northward into British America; . . . also in Europe and Asia."

B. PALLENS (Brid.) Röhl. *K.* 1959, at Ravine Creek, altitude about 10,600 feet. Its previously known distribution, according to Andrews

(1940) was "In wet places, from the far north, southward across the continent to northern New England, New York, Montana, Washington; also in Europe and Asia."

B. *PALLESCENS* Schwaegr. *Koch* 2211 (UM), near Bridgeport.

B. *STENOTRICHUM* K. Müll. *C.* 4787.

B. *TURBINATUM* (H.) Smith. *Alexander* (UC 719377), along Deep Creek; *C.* 47125; *Koch* 1772 (UM), Leevining.

B. *WEIGELII* Spreng. *C.* 47112, 47126.

LEPTOBRYUM *PYRIFORME* (H.) Schimp. *Cantelow* (LFK x105), near Bridgeport (CAS); *Hall* 502 (CAS 221851; UC), Leevining; *Koch* 1774 (UM), Leevining; *C.* 47158.

MNIOBRYUM *WAHLENBERGII* (W. & M.) Jenn. *C.* 4779, 47114, 47115.

POHLIA *CAMPTOTRACHELA* R. & C. R. R. *Koch* (LFK 2211), Barney Lake, (UM).

POHLIA *CRUDA* (H.) Lindb. *C.* 4792, 4798, 47147, 47159, the latter two from Leevining.

POHLIA *OBTUSIFOLIA* (Brid.) Koch. *C.* 47122, Middle Ridge near Spiller Lake, altitude at about 10,400 feet. Andrews (1940) used the name *P. cucullata* (Schwaegr.) Bruch. It has been reported from California only twice before (Koch 1950). Both reports are based on Bolander's collection from Mount Dana.

P. *DRUMMONDII* (C.M.) Andr. *C.* 47117.

#### MNIACEAE

MNIUM *MARGINATUM* (With.) P. B. *Koch* 1766 (UM), Leevining.

M. *MEDIUM* B. S. G. *Koch* 1775, 1767 (UM), Leevining.

M. *ORTHORHYNCHUM* Brid. *K.* 1917, 1920, above Alpine Lake, altitude about 11,300 feet. Andrews (1940) described it as "widely distributed through the 3 northern continents; in North America noted from Alaska and Yukon south to New Mexico, in the eastern states to North Carolina."

M. *PUNCTATUM* H. *Koch* 1768 (UM), Leevining.

#### AULACOMNIACEAE

AULACOMNIUM *PALUSTRE* (H.) Schwaegr. *C.* 4793, 47111; *K.* 1929, 2001.

#### BARTRAMIACEAE

BARTRAMIA *ITHYPHYLLA* Brid. *C.* 47136; *K.* 1930, 2003, 2012.

PHILONOTIS *AMERICANA* Dism. *C.* 4794, 4795, 4799; *Hall* 503 (NY), Leevining; R. R. *Koch* (LFK 2209), Barney Lake, (UM).

P. *FONTANA* (H.) Brid. *C.* 4778, 47102, 47104, 47106, 47124, 47131; *K.* 1908, 1935B, 1950, 1956; *Koch* 1779 (UM), Leevining; var. *PUMILA* (Turn.) Brid. *K.* 1975. The abundance of this moss undoubtedly reflects the absence here of the various species of *Sphagnum* which inhabit similar habitats in more northern latitudes.

#### ORTHOTRICHACEAE

AMPHIDIUM *LAPONNICUM* (H.) Schimp. *K.* 1982b, 1998.

ORTHOTRICHUM *LAEVIGATUM* Zett. *K.* 1919, 1921.

- O. LYELLII* var. *PAPILLOSUM* (Hampe) Lesq. & James. *C.* 474, 4757.  
*O. RUPESTRE* (Brid.) Schwaegr. *C.* 47158.

## FONTINALACEAE

- FONTINALIS ANTIPYRETICA* H. *C.* 4759, 4760.

## CRYPHAEACEAE

- DENDROALSIA ABIETINA* (Hook.) Britt. *C.* 47121.

## LEUCODONTACEAE

- ANTITRICHIA CALIFORNICA* (Hook. & Arn.) Sull. *K.* 1901.

## LESKEACEAE

- PSEUDOLESKEA PATENS* (Lindb.) Limpr. *K.* 1953, 1997.

## AMBLYSTEGIACEAE

- AMBLYSTEGIUM SERPENS* (H.) Schimp. *Koch* 1770 (UM) Leevining.

*CALLIERGON STRAMINEUM* (Brid.) Kindb. *K.* 1999, on eastern side of ridge between Big Horn Lake and East Pond, altitude about 11,100 feet. Previous records of this moss from California (Koch, 1949) were based on fragments gleaned from specimens of other taxa.

*CAMPYLIUM STELLATUM* (H.) Lange & C. Jens. *K.* 1990, at source of Cabin Creek, altitude about 10,350 feet. Although widely distributed in the boreal hemisphere, apparently the species has not been found in the Pacific Coast states before. Grout (1928–40) reported it as in "Northern U. S. and Canada; ranging west to the Rocky Mts., Colorado, British Columbia and Alaska; south to Pennsylvania and Ohio in the East."

*CRATONEURON FILICINUM* (H.) Roth. *Bolander* (NY), from Mono Pass (Lesq. 1868).

*DREPANOCLADUS EXANNULATUS* (Gümb.) Warnst. *C.* 47141; *K.* 2004.

*D. FLUITANS* (H.) Warnst. *K.* 1966, 1967.

*D. UNCINATUS* (H.) Warnst. *C.* 4791, 47100, 47133; *K.* 1905, 1926, 1994, 2005, 2008; *Koch* 1765 (UM), Leevining.

*HYGROHYPNUM LURIDUM* (H.) Jenn. *C.* 47128.

*H. MOLLE* (Schimp.) Loeske *C.* 47138; *K.* 1996, 2010.

*H. OCHRACEUM* (Wils.) Loeske *C.* 47118, 47119, 47120, 47127, 47153, the last from Leevining; *K.* 1969, 1976, 1977, 1978; *Koch* 1776 (UM) Leevining.

*H. SMITHII* (Lilj.) Broth. *C.* 4788.

*LEPTODICTYUM RIPARIUM* (H.) Warnst. *K.* 1970.

*L. TRICHOPODIUM* (Schultz) Warnst. *K.* 1963. According to Dr. Conard, this specimen is a variant of the species rather distinct from the following variety which is widely distributed elsewhere in California but not at high altitudes: var. *KOCHII* (B. S. G.) Broth. *C.* 47156, 47157; *Koch* 1771 (UM), all from Leevining. This variety has not been found in the Natural Area.



## BRACHYTHECIACEAE

*BRACHYTHECIUM ALBICANS* subsp. *occidentale* (R. & C.) Perss. *C. 47108*.

*B. ASPERRIMUM* Mitt. *C. 47140, 47149, 47151; Koch 1743* (UM), the latter three from Leevining.

*B. COLLINUM* Schimp. *K. 1906, 1936*.

*B. LAMPROCHRYSEUM* C. M. & Kindb. *Koch 1778* (UM), Leevining.

*EURHYNCHIUM STOKESII* (Smith) Schimp. *Koch 1780* (UM), Leevining.

*E. SUBSTRIGOSUM* Mac. *K. 1987; 1995*.

*HOMALOTHECIUM NEVADENSE* (Lesq.) R. & C. *C. 47134*.

*SCLERPODIUM OBTUSIFOLIUM* (Hook. & Wils.) Kindb. *C. 47150, 47154; 47155*, Leevining.

*S. TOURRETII* (Brid.) Koch. *Koch 1764* (UM), Leevining.

## HYPNACEAE

*HYPNUM REVOLUTUM* (Mitt.) Lindb. *K. 1922*, near Alpine Lake, altitude about 10,350 feet. Although Grout (1928-40) included California as being in the range of this species, the Ketchledge collection is the first I have seen (cf. Koch 1950).

## POLYTRICHACEAE

*POGONATUM ALPINUM* (H.) Röhl. *K. 2007, 2009*.

*POLYTRICHADELPHUS LYALLII* Mitt. *C. 47109, 47110; Baker 9128* (UM), near Lake Mamie; *Lewis* (LA), Saddlebag Lake.

*POLYTRICHUM JUNIPERINUM* H. *C. 4781, 47130; K. 1943; R. R. Koch* (LFK 2210), Barney Lake, (UM).

*P. PILIFERUM* H. *C. 4777, 4780, 47130; K. 1943*.

Division of General Studies,  
University of Illinois, Urbana.

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## REVIEWS

*The Future of Arid Lands.* Papers and Recommendations from the International Arid Lands Meeting. Edited by Gilbert F. White. 453 pp. Publication No. 43 of the American Association for the Advancement of Science, Washington, D.C., 1956. \$6.75 (\$5.75 to A.A.A.S. members prepaid).

The struggle of man toward utilization and productivization of arid areas is as old as agriculture. The fact that the main cradles of human civilization were situated in or near marginal areas forced the early agriculturists to understand the use of natural water resources and to economize them for rational irrigation farming. No wonder that hydrotechnical engineering of the ancient people, East and West, became world-famous for its relatively high level. However, it naturally reached its limits, and despite the ever-increasing world's population threatened by famine, one-third of the globe's surface remained for millenia condemned to sterility and desolation.

It was not until the advent of the present century that governmental and economical bodies began to show great interest in the question of utilization of arid zones for agriculture. Above all, it was the United Nations Educational Scientific and Cultural Organization which only recently internationalized this problem and both sponsored and organized conferences, symposia, and research programs, aiming at the development of arid zones. The organization brought together scientists of various disciplines to discuss problems of arid zone research and development possibilities in Turkey, India, Israel, England and elsewhere.

The book under review is the outcome of one of the recent symposia on arid land problems held in New Mexico between April 26 and May 4, 1955, in Albuquerque and in Socorro. Organized by the A.A.A.S. and supported by U.N.E.S.C.O. and other foundations, it consisted of three-day lectures. The aim of this symposium was to help in solving scientific and developmental problems of arid zones.

The book, edited by G. F. White, of the Department of Geography, University of Chicago, consists of thirty-four papers, most of them presented by United States scientists and a few by scientists from other countries. The book is divided into the following five sections: the first (pp. 3-64) deals with general problems of arid land development and planning of various aspects of future exploration lines. It consists of three articles by Schantz, Kellogg, and Dickson. The second (pp. 67-175) deals mainly with variability, fluctuation and predictability of water supply. Its subjects range from experimental determination of the water turnover to interpretation of climatic records, estimation of water supplies, drought cycles, and predictability of precipitation. The third (pp. 179-254), entitled "Better Use of Present Resources," deals with problems of improvement and restoration of grazing resources, increase of production, economizing water supplies, use of saline water, land erosion and reclamation, and limitation of land use. The fourth part (pp. 255-328), headed "Prospects for Additional Water Sources," deals mainly with the increase of water sources through demineralization of saline water, the induction of artificial precipitation, and the reuse of waste water. The fifth part (pp. 331-435) is concerned with problems of adaptation of plants and animals to arid conditions, selection of more productive plant and animal species, breeding of drought-resistant races, and the danger of locust invasion in desert grazing areas and cultivation patches. Concluding this part is a paper on desert agriculture in Israel, past and present, and research programmes conducted for productivization of the desert.

The concluding section of the book consists of thirty-one paragraphs of recommendations outlining future research on arid lands. They call for interdisciplinary cooperation and organization of research work in basic and applied science concerning arid land development. They include Meteorology and Climatology, Anthropology and Archeological Geography, Geology and Hydrology, Biology, Ecology, and Conservation.

The subject matter in the reviewed book is a very heterogeneous collection of lectures, ranging from archeology to genetics, from geography and geochronology

to plant physiology. The articles differ in length and coverage, some of them being preliminary, others very detailed. They present, however, an example of organizing data, methods, and ideas from very distinct fields of exploration toward the solution of this very complex problem, the future development of arid lands. This is the outstanding feature of this book.—M. ZOHARY, The Hebrew University, Jerusalem, Israel.

*Plants of the Pacific Northwest.* By LEONID ENARI. 315 pp., 185 figures. 1956. Binfords and Mort, Portland. \$3.00.

According to the author's preface, this book is "intended for the use of college students in elementary courses in botany or biology, high school students, and amateurs out of educational institutions who often find the standard manuals of plant identification too technical." To this end, Dr. Leonid Enari, formerly an associate professor at the University of Portland and now on the staff of the Los Angeles State and County Arboretum, has constructed an easily used key to 663 native or introduced herbs and woody plants of the Pacific Northwest. For the botanically untrained, the technical language of the keys of many contemporary manuals is a formidable barrier to their use. However, Dr. Enari has based his key on floral and vegetative characteristics which can be seen without the aid of a hand-lens, and the use of technical terms is held to a minimum. The artificial key leads the user directly to species determinations, although in the text the genera are grouped under family headings.

Another convenient feature of the book is that the glossary of terms and the illustrations of plant parts are inserted next to the key. The illustrations are simple line drawings by the author; those accompanying the text are primarily outlines of single leaves of several of the species. Some of the few habit sketches included have apparently suffered from reduction in printing, and some of the lines are obscured by running of the ink.

The species are numbered in the key, and are listed in the same numerical sequence in the text. Each species is listed by both its Latin binomial and one or several common names. Following the names is a short, synoptic description of the plant and its habitat, although geographical range is not given. Appended to the text are separate indices to the Latin and English names of the plants. Typographical errors are few, and none is very serious. The book is attractively bound in green cloth, popularly priced, and small enough to be carried conveniently in the field.

This book will appeal to the amateur interested in identifying the conspicuous plants of the Pacific Northwest; its greatest recommendation is its simple and easily used key. Once the fundamentals of using this key are in hand, it will be a relatively painless transition to the more technical floras and manuals of the region covered.—

ROBERT ORNDUFF, Department of Botany, University of California, Berkeley.

*Portraits from Memory. Recollections of a Zoologist.* By RICHARD B. GOLDSCHMIDT. 181 pp., 13 figs., 1956. University of Washington Press. \$3.50.

These "recollections of a zoologist" should be greeted with enthusiastic appreciation by all biologists. All of us are concerned with the history of that body of facts and principles whose formulation or discovery began with Strasburger's description of mitosis, 1875, and was completed (in the sense that the enormous mass of subsequent discovery had added more to detail than to principle) by the adequate inductive establishment of the chromosome theory of heredity by Morgan and his associates, 1915. The facts are drawn indifferently from flies, maize, or molds; the principles apply alike to all nucleate organisms; the personalities of the scientists who established them should be interesting to all of their successors.

Goldschmidt was the pupil of several of the first founders of this body of science, and is himself noted, among other things, for studies of sex intergrades in moths and for the opinion that genes (in the usual sense of the word, designating some sort of discrete bodies) do not exist. Exiled by a tyrant on grounds of "race," he was made

welcome in this country. These happenings have the incidental effect, that his book is written in our language.

An introductory chapter describes the university system under which German science became great: administration, so far as it existed, elected by the faculty; departments of education restricted to part of one year's instruction of those Doctors of Philosophy who were to staff the secondary schools. In the personal reminiscences which make up the bulk of the work, the accounts of Bütschli, O. Hertwig, R. Hertwig, Boveri, Schaudinn, and Prowazek are particularly full, and are marked by evident affection.

The writer of this review was particularly interested by reference to an unhappy piece of personality involved in the discovery of mitosis. At about the middle of the stretch of time which has elapsed since this discovery, I took careful notes upon the lectures of an eminent cytologist, a pupil of Strasburger; including at one point the following passage:

"Schneider deserves the credit for discovering mitosis, but . . . and Strasburger have always received it. Strasburger's story is as follows: he discovered mitosis, but foolishly showed it to his friend . . . The latter got a leave of absence from the university, went to Italy, and published his book, *Zellbildung und Zelltheilung*, in '75, a few months before Strasburger published his. . . would doubtless tell a different story."

This account is erroneous upon its face. I have assured myself, by correspondence with former fellow students and with very little personal satisfaction, that the confusion was in the lectures, and not in the note-taking. Goldschmidt's reference to the same incident is as follows:

"Bütschli told me—and in view of his character there can be no doubt of the truth of his words—that at first Strasburger could not interpret his slides of dividing plant cells. At that time he learned that Bütschli was doing similar things and visited him (Bonn and Frankfurt are not far apart). Bütschli demonstrated his material and discussed his interpretations, and this first opened Strasburger's eyes. But, while Bütschli kept adding still more facts, Strasburger published his first report."

Thus Strasburger's pupil and Bütschli's agree that Strasburger let his observations be known to a colleague, undoubtedly Bütschli. We do not have to believe that Strasburger was unable to understand what he had seen. Surely he was within his rights in bringing his observations quickly to publication. It remains a reasonable possibility that Bütschli was justified in resenting a failure to acknowledge cooperation which had been genuinely important.—H. F. COPELAND, Sacramento Junior College.

*Edward Palmer, Plant Explorer of the American West.* By ROGERS McVAUGH. 430 pp., 12 plates, 2 maps. 1956. University of Oklahoma Press, Norman. Cloth, \$6.00.

Parry, Pringle, and Palmer compose a triumvirate in the botanical exploration of the American West. Parry's part in the discovery of new species in the days when Asa Gray and colleagues were busily describing the floras of the West remains to be told; Pringle's story has been detailed (at least for his important Mexican years) by Miss Helen Davis in 1936. Now Professor McVaugh of the University of Michigan has provided a biography of Edward Palmer (1831–1911). Palmer is considered less important than either Parry or Pringle, if inclusion in the *Dictionary of American Biography* is a significant test. Like Parry, Palmer was born in England, though less identified with British botany than Parry, who took pains to forward his collections to Kew, and to keep in touch with Hooker. Palmer was either self-effacing or the victim of poor luck in winning recognition in this country. Other botanical explorers were more than once the foci of important reports on the floras of the western states, but with few exceptions Palmer's discoveries were only incidentally noticed in the course of the reporting on the collections of others. Only for Palmer's pioneering explorations on Guadalupe Island off the Mexican coast was there special recognition. It seems especially difficult to determine the personality of Edward Palmer, whereas of Parry and Pringle we know good stories and revealing remarks. In a long series

of letters from Parry to Harry Norton Patterson of Oquawka, Illinois, often stuffed with gossip news of botanists, there is scant mention of Dr. Palmer (Kibbe, Alice L., *Afield with plant lovers and collectors*. pp. 172-205. 1953. Carthage, Ill.). Misfortune befell Palmer now and again in his field collecting, as when Parry decries in his letter of April 11, 1879, that there "came another batch from Palmer, made on his route home from San Luis [Potosi] to Tampico. They are generally in very bad condition, hardly fit for herbarium specimens, and I do not think best to include them in the sets." Indifferent health, too, plagued Palmer. Parry wrote under date of September 7, 1888, "Dr. Palmer is out here, but is not able to collect much." Palmer seemed to miss the joy of collecting, for instance, that Pringle felt when, west of the city of Chihuahua, he wrote: "in the afternoon I went down to the river for a bath and brought home with me at dark 1211, *Dalea filiformis* Gray, 1436 *Bouteloua bromoides* Lag., and 1251 *Prionosciadium madrese* Wats., n. gen., and 1400 *Scirpus pringlei* Wats. n. sp." A new genus and a new species are a happy ornament to any bath, a kind of shower of glory.

In his life Palmer was never one of the restless, striving sort. All his urgency and strenuousness he reserved for his collecting. As John Burroughs said of Whitman, "he seems always to have been a sort of visitor in life, noting, observing, absorbing, keeping aloof from all ties that would hold him."

One of the few recorded anecdotes of Palmer comes, not from McVaugh, but from that raconteur Edmund Jaeger (*Desert wild flowers*, ed. 2, p. 207. 1941. Stanford.). Returning from a trip that Palmer made with Parry and Lemmon to San Gorgonio Peak, the highest mountain in southern California, in May, 1876, he fell from his horse and severely injured his spine. He was left on an improvised litter while the party returned for assistance down the mountain. Meanwhile the San Bernardino newspaper reported that Dr. Palmer had been left "on the mountain without grass or water with a man to look after him." For some time afterwards he was greeted as "the man who had been left on Grayback [the local name of the mountain] without grass or water." Or, by others, "Hello! Old grass and water! How's your back?" This meeting with Parry and Lemmon was, in fact, a momentous week, for though Palmer had become acquainted with Parry in 1870, if not before, they had not been in the field together. Later they were to botanize together in Mexico. Lemmon had come to the winter resort of Crafton to join Dr. Parry for exploration of the San Bernardino Mountains. Parry evidently found Lemmon an agreeable companion for he wrote Patterson on January 2, 1879, that Lemmon was "an excellent botanist and good fellow otherwise." Dr. Palmer never elicited such a verdict from Parry.

Palmer was an indefatigable collector (though McVaugh doubts that he ever really 'enjoyed' collecting). His specimens were inferior to Pringle's and often subsequent in time to Parry's for Colorado, southern California, and the Mexican borderlands. But for Mexico Standley says that "his collections are surpassed in extent, probably, by those of no other collector." By Safford's count 1,162 species of flowering plants were first made known to science from his specimens—a notable record indeed! Sereno Watson resorted to anagrams in the course of describing Palmer's new genera, witness *Malperia*. Palmer told Tidestrom that on one occasion when he visited Harvard Asa Gray exclaimed, "Watson, here comes Palmer, get out the register of new species."

Palmer's bird collections have been extensively noticed by Joseph Grinnell (A distributional summation of the ornithology of Lower California. Univ. Calif. Publ. Zool. 32: 1-300. 1928) for Lower California, including the Guadalupe Island species, some now extinct. A short note published in *Entomological News* at his death refers to his insect and other zoological collections preserved at Harvard and Washington. When his zoological collections are included in the total, the number of types based on Palmer's material must surely exceed two thousand species, an accomplishment that can never be repeated for this continent.

Palmer's ethnobotanical contribution was of the first importance, though not

stressed by McVaugh. Walter Hough wrote at Palmer's death that the value of his collections rested "in the early period of their acquisition and the care with which the data and the method of procuring them were recorded." He "made the first exploration of an ancient pueblo ruin, in 1873, a mound at St. George, Utah, preserving every fragment of evidence that came under his trowel and carrying out the exploration with a skill and perfection of method that have not been surpassed in that field." This assiduous collector brought together "some of the most unique specimens ever obtained from the Apache," and, altogether, his ethnological material is accounted among the most valuable in the United States National Museum. In writing of such subjects as sand-fool (*Ammobroma sonora*), Palmer was careful to cite the Indian name, *biatatk*, and its procurement and use.

Any sketch of Palmer must be a pedestrian account. McVaugh's biography itself is brief, amounting to 122 pages of the book. The narrative is, in fact, an extended annotated itinerary through life rather than a portrait. It is perhaps impossible to uncover the portrait of the man Palmer. His friends, sponsors, competitors, cronies, Indians, and a very few ladies are identified in on-the-spot footnotes. Dinah Riches, his English bride who accompanied him on the transatlantic run of the *Amazon*, out of London docks April 16, 1856, drops from the Palmer story with the fall of the anchor in New York harbor. McVaugh justly remarks that this event ranks "among the most intriguing incidents of his life."

Following the biographical portion of the book is a 230-page gazetteer of collecting localities, giving the precise location in terms of seventy-five maps checked for their inclusion. This 'geographical index' will prove immensely useful for placing not only Palmer's localities but for others of his period. Some of us will shelve this book beside the atlases, directories, and nomenclators for ready reference. The photographic illustrations animate the book and there are two unusual maps. JOSEPH EWAN, Department of Botany, Tulane University, New Orleans.

#### NOTES AND NEWS

**VARIABILITY IN *TRILLIUM OVATUM* PURSH.** This *Trillium*, so readily recognized, is nevertheless subject to frequent striking variations. Normally the three leaves are approximately equally spaced, separated by angles of 120°. However, it is fairly common to find plants in which two of the leaves are directly opposed, i.e., making an angle of 180°, while the third leaf is inserted on one side, perpendicular to the common axis of the other two. This suggests that some ancestor may have had four leaves, and indeed, one plant (unfortunately sterile) was seen which *had* four leaves, of approximately the same size and equally spaced.

Occasionally plants are seen which are 2-merous, sometimes imperfectly so (one plant had one normal leaf and one leaf which was divided about one-fourth of its length from the apex), but sometimes they are completely and perfectly 2-merous. One plant which was perfectly 2-merous throughout was transplanted for further observation, and the next year the root sent up two stalks, both of which were normal and perfectly 3-merous! In another year this root again produced a 2-merous plant, although not so perfect as the first one had been.

At one station plants were observed to produce, year after year, flowers which had crumpled and imperfect petals in addition to and inside the three normal ones.

These tendencies toward variability in *Trillium ovatum* suggest an inherent genetic instability.—VESTA F. HESSE, Boulder Creek, California.

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Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

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# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 7

JULY, 1958

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PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

# MADROÑO

## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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THE TAXONOMY OF THE SPECIES COMPLEX,  
STREPTANTHUS GLANDULOSUS HOOK.A. R. KRUCKEBERG<sup>1</sup>

The taxonomic delimitation of species and their infraspecific elements by experiment has nurtured a vigorous renaissance in biological taxonomy. Nevertheless, taxonomic revision has not been the sole objective of experimental studies of wild populations. Often, a revision may be merely a useful by-product of a study aimed at other objectives. The present review of the taxonomy of *Streptanthus glandulosus* Hook. came into being in such a fashion.

While investigating the extent of genetic isolation between certain populations of the central Californian serpentine species, *Streptanthus glandulosus*, the author discovered that genetic isolation between some populations was complete and between others only partial. Moreover it was observed that complete genetic isolation for such populations was often correlated with their geographic isolation and morphological distinctness. Here then were available three basic criteria for the demarcation of species. The presence of discontinuities in the variation pattern of *S. glandulosus* permits treating these biologically isolated populations as taxonomic entities. The experimental evidence for the taxonomic disposition of the members of the complex as species or subspecies is reported in detail elsewhere (Kruckeberg, 1957).

The taxonomy of the entities comprising the *Streptanthus glandulosus* complex has had a complicated history. The Hooker epithet of *S. glandulosus* was applied to plants collected by Douglas in California and remained the only taxon for the group until the time of E. L. Greene. Greene described twelve species within the *glandulosus* pattern of variation, eleven of which he placed in a new genus, *Euclisia* (Greene, 1906). Adopting more conservative views, Jepson (1925, 1936) and Abrams (1944) recognized only three species in the complex: *Streptanthus glandulosus* with two varieties [var. *albidus* (Greene) Jeps., and var. *pulchellus* (Greene) Jeps.], *S. niger* Greene, and *S. secundus* Greene. A recent re-evaluation of *S. glandulosus* is found in an unpublished monograph of the section *Euclisia* by Morrison (1941). He recognized as the subsection *Pulchelli* of the section *Euclisia*, two species, *S. glandulosus* and *S. Coombsae* Eastwood. Morrison defined *S. glandulosus* broadly to include five subspecies: "*typicus*," *albidus*, *niger*, *pulchellus*, and *secundus*. This treatment of the complex accounted for the taxa recognized by Greene by treating certain of them as infraspecific elements of a polymorphic species complex and by relegating others to synonymy.

<sup>1</sup> A portion of this study was financed by grants from the state of Washington initiative No. 171 and the National Science Foundation.

Very little is known about *Streptanthus Coombsae*, since it has not been collected subsequent to its discovery in 1913 by Mrs. A. L. Coombs. Eastwood (1931) cited it as being collected "on the Williamson River, Southern Oregon." The only river in Oregon by this name is in the arid sagebrush country east of the Cascade Range in Klamath County, a most unlikely habitat for members of the section *Euclisia*, most of which occur on serpentine outcrops in cismontane California. However, members of the section *Euclisia* do occur in southwestern Oregon, growing on serpentine areas in Josephine County. *Streptanthus Coombsae* is not dealt with further in the present paper.

The present revision of the *Streptanthus glandulosus* complex is based on the premise that the degree of taxonomic relationship may be inferred from the degree of compatibility between different populations or from fertility of interpopulational hybrids. Accordingly, the taxonomic implications of hybrid fertility have been evaluated for over 300 artificial crosses involving 32 different population samples of the *S. glandulosus* complex in various combinations. The results and implications of this analysis were published by the author (Kruckeberg, 1957). Three of the eight taxa recognized here are regarded as species. These are *S. niger* Greene, *S. albidus* Greene, and *S. glandulosus* Hooker. In the previous treatments of Jepson, Abrams, and Morrison, *S. albidus* has been regarded as an infraspecific element of *S. glandulosus*. However, the sharp genetic discontinuity between *S. albidus* and all other populations, coupled with the morphological distinctness and regional restriction of *S. albidus* warrant the restoration of this Greeneian species. Similar justification can be made for the recognition of *S. niger*, a species of very narrow serpentine restriction. *Streptanthus glandulosus* is here taken as the most widespread and polymorphic of the three species. It occurs discontinuously and mainly on serpentine from Josephine County, Oregon to San Luis Obispo County, California. Three subspecies of *S. glandulosus* are recognized on the basis of more or less well-delimited morphological discontinuities and geographic range, coupled with high average inter- and infrasubspecific fertilities in interpopulational hybrids. They are *S. glandulosus* subsp. *glandulosus*, subsp. *pulchellus*, and subsp. *secundus* (with three varieties). Figure 1, taken from Kruckeberg (1956), summarizes the interrelationships of the major taxa constituting the *S. glandulosus* complex.

The elements taken here as constituting the *Streptanthus glandulosus* complex can be distinguished from other members of the section *Euclisia* by a particular ensemble of characteristics. The leaves are narrowly lanceolate and sinuately toothed to pinnatifid. The herbage is usually pubescent at least in the rosette stage, often densely hispid (*S. niger* is the only exception, with consistently glabrous and glaucous foliage). In contrast to the "color-spot" species where the terminal flowers of the raceme are sterile and their sepals highly colored and elongated, the members of the *S. glandulosus* complex produce solely fertile flowers which

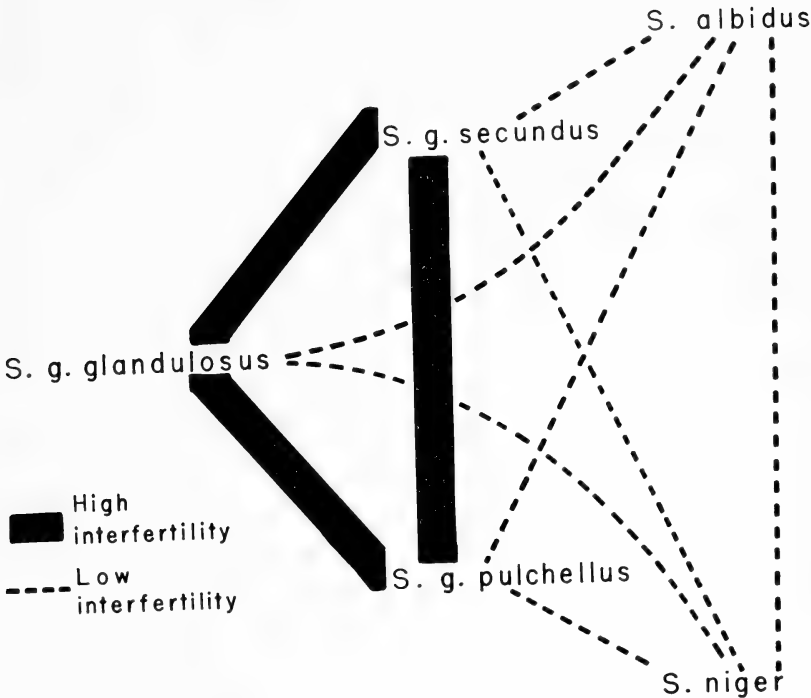


FIG. 1. Summary of the interfertility relationships among the five taxa of the *Streptanthus glandulosus* complex. A synthesis of pollen fertilities from over 300 artificial interpopulational hybrids.

become only slightly smaller towards the terminal flower. Thus the combined features of leaf shape, pubescence, and inflorescence serve to set the complex apart from other "euclisian" streptanthi. All members of the complex have the gametic chromosome number of 14.

A key to the five taxa permits the identification of the majority of populations. It must be recognized, however, that we are dealing with an intricate pattern of variation that appears to be correlated with the spatial isolation of populations (Kruckeberg, loc. cit.). In other words, the discontinuity of suitable habitats has promoted many morphologically distinct populations of a very local occurrence. Thus the eternal dilemma is forced upon us of either having to recognize taxonomically each Mendelian population or abstracting from the total variation pattern only the more salient representations. The latter course has been adopted here as best serving the needs of a practical taxonomy. At the same time attention is called to the fact that certain of the taxa (especially *S. glandulosus* subsp. *glandulosus* and *S. glandulosus* subsp. *secundus*) encompass systems of populations with variable morphology and showing varying degrees of genetic isolation.

KEY TO THE SPECIES AND SUBSPECIES IN THE *STREPTANTHUS GLANDULOSUS* COMPLEX

- A. Plants glabrous throughout; inflorescence simple or branched, forming a "zig-zag" outline; pedicels twice as long as the purplish-black flowers; serpentine outcrops, Tiburon Peninsula, Marin County.....3. *S. niger*
- AA. Plants pubescent at least on the basal and lower cauline leaves; inflorescence straight and stiffly erect, simple or branched; pedicels shorter than the flowers.
  - B. Inflorescence a second, simple or branched, raceme; Marin County and northward in the outer Coast Ranges to west-central Sonoma County.
    - C. Sepals greenish-white, white, or yellow (or rarely rose); petals colored like the sepals or veined with rose or purple; inflorescence not crowded; plants usually tall, 3-7 dm. high; usually on serpentine, Marin and Sonoma counties, and possibly discontinuous northward along the outer Coast Ranges to Josephine County, Oregon.....1c. *S. glandulosus* subsp. *secundus*
    - CC. Sepals reddish-purple; flowers crowded on the short inflorescences; plants usually dwarfish, 1-4 dm. high; on serpentine outcrops, south and east slopes of Mount Tamalpais, Marin County
      - 1b. *S. glandulosus* subsp. *pulchellus*
  - BB. Inflorescence not second.
    - D. Plants robust, 6-10 dm. tall; herbage coarse, often fleshy, glaucous and nearly glabrous; flowers either lilac-lavender or white; usually on serpentine, Alameda, Contra Costa and Santa Clara counties.
      - E. Flowers greenish-white; on serpentine hills south of San Jose, Santa Clara County.....2a. *S. albidus* subsp. *albidus*
      - EE. Flowers lilac-lavender; on barren outcrops of various parent materials, Alameda, Contra Costa, and Santa Clara counties.
        - 2b. *S. albidus* subsp. *peramoenus*
    - DD. Plants smaller, 3-7 dm. tall; herbage green, sparsely pubescent to hispid; flowers lilac-lavender to purple or purplish-black, rarely pale rose; widely distributed mainly on serpentine from San Luis Obispo County north to Tehama County.....1a. *S. glandulosus* subsp. *glandulosus*

1. *STREPTANTHUS GLANDULOSUS* Hook. Ic. Pl. 1, pl. 40. 1836.

Annual; stems erect, simple or divaricately branched just above the basal rosette, glabrous or sparingly (rarely densely) hispid to the inflorescence; plants densely rosulate at first, basal leaves 5-10 cm. long, hispid, narrowly lanceolate, tapering to a short, winged petiole, coarsely and sinuately toothed to shallowly pinnatifid, the teeth callus-tipped; cauline leaves sessile, auriculate, narrowly lanceolate, remotely toothed, gradually reduced upwards, becoming entire, auriculate, lanceolate-acuminate; by anthesis basal and lower cauline leaves becoming deciduous and stems ultimately naked up to 2-3 nodes below the inflorescence, flowers 0.8-1.2 cm. long, ascending to erect in single to several open, erect racemes; at anthesis flowers on wiry pedicels 1.0 cm. long, spaced at intervals of 4 to 2 cm. from base to apex; sepals glabrous or sparingly hispid, wholly or partly connivent, strongly keeled and collectively umbilicate at base, the calyx thus appearing inflated; petals well exerted; the crisped margins usually white, the upper pair with a broad blade, slightly to strongly recurved, longer than the lower, less recurved and narrower pair; stamens in three pairs, the upper with filaments connate to  $\frac{1}{2}$  -  $\frac{3}{4}$  their length, bearing sterile or scarcely polliniferous anthers,

the lower and lateral pair fertile, extending and dehiscent in that order, scarcely exerted; siliques glabrous (or rarely hispid), not torulose, 5–8 cm. long, straight and ascending, or divaricate, to arcuate or sharply reflexed; seeds oblong-oval, winged, 2–2.5 mm. long, 1.0–1.5 mm. wide; cotyledons accumbent (*vide* F. W. Hoffman).

1a. *STREPTANTHUS GLANDULOSUS* subsp. ***glandulosus***. *S. glandulosus* Hook., Ic. Pl. 1. pl. 40. 1836. Type: *Douglas*, Monterey, California. *Erysimum glandulosum* O. Ktze., Rev. Gen. 2: 933. 1891. *Euclisia glandulosa* Greene, Leaf. Bot. Obs. 1: 82. 1904.

*S. biolettii* Greene, Pittonia 2: 225. 1892. Type: *Bioletti*, on Hoods Peak in 1889. *Euclisia biolettii*, Leaf. Bot. Obs. 1: 83. 1904.

*S. versicolor* Greene, Erythea 3: 99. 1895. Type: *Byxbee*, banks of Navarro River in 1894. *Euclisia versicolor*, Leaf. Bot. Obs. 1: 83. 1904.

*S. asper* Greene, Pittonia 3: 225. 1897. Type: *Greene*, on Mount St. Helena in 1894. *Euclisia aspera*, Leaf. Bot. Obs. 1: 83. 1904.

*S. bakeri* Greene ex. C. F. Baker, West Am. Plants, 2: 17. 1903. Type: *Baker*, near Bethany on plains of upper San Joaquin, 1903. *Euclisia bakeri*, Leaf. Bot. Obs. 1: 84. 1904.

*S. mildredae* Greene, Leaf. Bot. Obs. 1: 83. 1904. Type: *Holden*, Mount Hamilton. *Euclisia mildredae*, Leaf. Bot. Obs. 1: 83. 1904.

*Euclisia violacea* Greene, Leaf. Bot. Obs. 1: 83. 1904. Type: *Palmer*, "somewhere in middle California," 1876; *US* 4297!

*Euclisia elatior* Greene, Leaf. Bot. Obs. 1: 84. 1904. Type: *Vasey*, Santa Lucia Mountains, in 1880; *US* 4295!

Flowers lilac-lavender to purple or more often purplish-black, rarely rose.  $n=14$ .

Type. "Monterey, California," *Douglas* as figured by Hooker (1836). Of the type, E. L. Greene (1904, p. 82) stated: "*S. glandulosus*, Hook . . . , as to original specimens, but figures false. *Streptanthus peramoenus*, Greene, . . . I did not believe that the plant with the remarkably irregular calyx described by me could be that which had been intended by Hooker's figure until I had seen the originals of *S. glandulosus* at Kew. Such falsification of the characters of a species is not publication; and this beautiful plant was truly first described, and therefore published, as *S. peramoenus*, which name ought to be continued in use, and Hooker's suppressed as being worse than a *nomen nudum*." However, Jepson evidently had no misgivings about the Hooker name when he annotated a specimen assigned to one of Greene's many segregates of subsp. *glandulosus* (i.e., *S. biolettii*) as follows: "Identical with *S. glandulosus* Hook.! Compared at Gray Herbarium with the cotype.—W.L.J." (UC 10874).

Range and Variation. The subsp. *glandulosus* constitutes the major element of the species and as such has the most extensive distribution. Within its north-south range from Tehama County to San Luis Obispo County, there may be blocked out areas of morphological homogeneity, although these are not always clear-cut. Plants with large, lilac-lavender

flowers on a thick-set peduncle occur in the southern end of the range—mainly in northern San Luis Obispo County. Northward from Monterey County, the transition is rather abrupt and the inflorescences are typically more delicate, with flowers that are either violet-purple or more commonly purplish-black. The blades of the petals are white along their crisped margins, with the median portion of the lamina veined in violet or purple. South of San Francisco Bay, the dark-flowered form of subsp. *glandulosus* is found chiefly on serpentine in Monterey, Santa Cruz, San Benito, and Stanislaus counties; a very few collections of this form are from southeastern Alameda County in the Bay region. North of the Bay, the distribution of the dark purple-flowered plants is mainly on serpentine outcrops in the mountains and foothills bordering the Great Valley, and occasionally westward to the outer Coast Ranges. This dark-purple form from north of the Bay has been collected most frequently in Napa and Lake counties, and to a lesser extent in eastern Sonoma, Solano, Colusa, Tehama, and Mendocino counties.

Specimens seen. San Luis Obispo County: 3.6 miles northeast of Valencia Peak, *Belshaw* 1727 (UC) (17)<sup>2</sup>. Monterey County: granite talus, east side of Henry Sands Canyon road, Gabilan Range, 2772 (UC) (5). Santa Cruz County: Charmichael's Mill, Santa Cruz Mountains, *Pendleton* 943 (UC) (1). San Benito County: trail above weather station, Pinnacles National Monument, Paicines, *Burgess* 172 (UC) (1). Stanislaus County: Del Puerto Canyon *Hoover* 3374 (UC) (3). Santa Clara County: Copernicus Peak, Mount Hamilton, *Sharsmith* 1287 (UC) (14). Alameda County: Mocho Creek, *Elmer* 4415 (UC) (2). Sonoma County: serpentine along ridge-top above Pine Flat and near Contact Mine, *Hoffman* 2902 (UC) (8). Napa County: Pope Creek bridge south of Walters Springs, *Keck* 2370 (UC) (11). Lake County: oak forest, Bartlett Mountain, 4 miles from Lucerne, *Mason* 11747 (UC) (24). Solano County: Weldon Canyon road north of Vacaville, *Gould* 262 (UC) (3). Colusa County: grade on Rumsey-Arbuckle road, *Hoover* 3205 (UC) (4). Mendocino County: serpentine talus 0.9 miles west of Hopland, *Hoffman* 2274 (UC) (4). Tehama County: 5½ miles west of Paskenta in foothills near a burn, *Baker* 12539 (UC) (1).

1b. *STREPTANTHUS GLANDULOSUS* subsp. **pulchellus** (Greene) Kruckeberg hoc loc. *S. pulchellus* Greene, Pittonia 2: 225. 1892. Type: *Howe*, dry ridges on the southern flank of Mount Tamalpais, 1892. *Euclisia pulchella*, Leaflet Bot. Obs. 1: 83. 1904. *Streptanthus glandulosus* var. *pulchellus* Jepson, Man. Fl. Pl. Calif. 420. 1925.

Plants often dwarfish, 1–4 dm. tall, flowers reddish-purple, usually secund, crowded on the short, simple to branched racemes; siliques divaricate or ascending, 4–6 cm. long. *n* = 14.

<sup>2</sup> One specimen for each county is cited; the total number seen from a given county is given in parentheses.



Range and Variation: Subspecies *pulchellus* is confined to serpentine outcrops on the slopes of Mount Tamalpais, Marin County. The combination of dwarfish stature, purple flower color and secund inflorescence serves to distinguish subsp. *pulchellus* from the other subspecies. It is, however, highly interfertile with the Marin County populations of subsp. *secundus*, as well as with certain Napa and Lake County populations of subsp. *glandulosus*. Two other species of the section *Euclisia* occur in Marin County. With *S. niger*, subsp. *pulchellus* is both spatially and genetically isolated. With the equally narrow endemic, *S. batrachopus* Morrison, it is sympatric, but as yet no attempt has been made to cross these two very different plants.

Specimens seen. Marin County: Large serpentine outcrop between Mountain Theater and the toll road, Mount Tamalpais, *Morrison 3103* (UC) (21).

1c. STREPTANTHUS GLANDULOSUS subsp. **secundus** (Greene) Kruckeberg hoc loc. *S. secundus* Greene, Fl. Fran. 261. 1891. Type: *Greene*, north base, Mount Tamalpais, 1886. *Euclisia secunda* Greene. Leaf. Bot. Obs. 1:83. 1904.

Flowers in open or crowded secund racemes; siliques usually arcuate, 5–6 cm. long.

1d. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **secundus**. *S. secundus* Greene, Fl. Fran. 261. 1891. *Euclisia secunda* Greene, Leaf. Bot. Obs. 1:83. 1904. (*Greene*, north base, Mount Tamalpais.)

Flowers greenish-yellow, tinged with rose or purple as blotches at the base of the sepal and on the veins of the petal lamina.  $n = 14$ .

Range. Mostly on serpentine, north side of Mount Tamalpais and the adjacent grassy or chaparral-covered hillsides of Marin County.

Specimens seen. Marin County: Serpentine slope at head of Lucas Valley, *Howell 13945* (WTU) (13).

1e. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **sonomensis** Kruckeberg hoc loc. *Hoffman 2323* (UC 985963) serpentine, Great Eastern Quicksilver Mine, near Guerneville, Sonoma County, June 8, 1948.

Floris luteis vel viridio-alba vel alba.

Flowers yellow, white or greenish-white.  $n = 14$ .

Range. On serpentine or other ecologically similar sites in central Sonoma County, ranging from the eastern border of the county (west end of Knight's Valley) to Cazadero in the western section of the county.

Specimens seen. Sonoma County: 3 miles south of Monte Rio on road to Camp Meeker, *Hoover 5084* (UC) (24).

1f. STREPTANTHUS GLANDULOSUS subsp. SECUNDUS var. **hoffmanii** Kruckeberg hoc loc. *Constance 2155* (UC 614606) moist soil of steep, rocky, nonserpentinized bank with *Umbellularia* and *Aesculus* at edge of Sequoia grove, 400 feet altitude, Russian Gulch, 8 miles south of Fort Ross, Sonoma County, April 24, 1938.

Floris roseis vel roseo-purpureis.

Flowers rose to rose-purple.  $n = 14$ .

Range. Open, rocky slopes of either serpentine or non-serpentine parent material. Known from only the type locality and Red Slide at the headwaters of Austin Creek, both areas just back of the wooded ridges along the coast.

Specimens seen. Sonoma County: serpentine, Red Slide at headwaters of East Austin Creek, *Hoffman 2343* (UC) (3).

Range and Variation of subsp. *secundus*. Subspecies *secundus* occupies a well-defined territory extending from the north side of Mount Tamalpais, Marin County, north throughout most of Sonoma County. The flowers of the Marin County plants (var. *secundus*) have greenish-white calyces and yellowish petals, but with both sets of parts prominently veined with violet, while the flowers of the Sonoma County plants (var. *sonomensis*) are either pure yellow or greenish-white. The center of distribution of subsp. *secundus* appears to be just north and south of the Russian River around Guerneville, where it occurs predominantly on serpentine, as var. *sonomensis*.

The rose-colored plants (var. *hoffmanii*) have been collected only rarely in the little explored Russian Gulch-Austin Creek areas north of the Russian River. The collections of the enthusiastic *Streptanthus* specialist, Freed W. Hoffman, of Guerneville, have added materially to our knowledge of the flora of this little known region. Variety *hoffmanii* has the most delicate inflorescences of all the forms of *S. glandulosus*, a character easily singled out in garden cultures where it can be compared with the inflorescences of plants from other populations. As was pointed out in Kruckeberg (1956), the high interfertility of this form with Sonoma and Lake County plants of both subsp. *glandulosus* and subsp. *secundus*, make it difficult to place these rose-colored populations in one or another of the subspecies. The second inflorescence and the distribution of the variety justify its alliance with subsp. *secundus* here.

The recognition of two regional facies of the subspecies, one in Marin County (var. *secundus*) and the other in Sonoma County (var. *sonomensis* and var. *hoffmanii*), is supported by the fact that interpopulational hybrids between plants from the two areas are less fertile than those involving populations within the two areas.

Populations in Josephine County, Oregon, which are readily referable to the *S. glandulosus* complex, are, nevertheless, anomalous in their relation to subspecies *secundus* and *glandulosus*. These plants from Oregon most resemble the Marin County variety of subsp. *secundus*. Yet the gap in distribution of subsp. *secundus* between even the northern Sonoma County plants and the southern Oregon ones is both absolute and wide. Hybrids between the Oregon plants and plants of Californian *S. glandulosus* do not clarify the affinity of the Oregon plants to one or another of the three subspecies, since exceptionally fertile hybrids have been obtained in a number of these crosses. The taxonomic position of the Oregon plants

will remain in doubt until collecting of streptanthi throughout the serpentine of northern California and southwestern Oregon is intensified and until the fertility of the appropriate interpopulational hybrids is evaluated.

2. *STREPTANTHUS ALBIDUS* Greene, Pittonia 1:62. 1887.

Habit similar to *S. glandulosus*, but usually taller (6–10 dm. high), stout, tending to be fleshy and glaucous throughout; rosette leaves sinuately dentate, callus-tipped, sparsely pubescent, or more commonly, glabrous, broadly linear-lanceolate, 9–12 cm. long; cauline leaves similar but gradually shorter upwards, saggitate-clasping; flowers large, 1.4 cm. long (between distal ends of reflexed upper and lower petals) and 1.7 cm. wide; petals strongly recurved, the margins of the blade crisped and usually white; siliques straight, stiffly and divaricately ascending, 6–8 cm. long; seeds as in *S. glandulosus*.

2a. *STREPTANTHUS ALBIDUS* Greene subsp. **albidus** *S. albidus* Greene, Pittonia 1:62. 1887. Type: *Rattan*, hillsides four miles south of San Jose, in 1887. *Euclisia albida*, Leaflet. Bot. Obs. 1:83. 1904. *S. glandulosus* var. *albidus* Jepson, Man. Fl. Pl. Calif. 419. 1925.

Sepals greenish white, tawny purple-tinged at base.  $n = 14$ .

Specimens seen. Santa Clara County: Metcalfe Canyon,  $1\frac{1}{4}$  miles northeast of Coyote, *Sharsmith* 3956 (UC) (8); photograph of isotype seen.

2b. *STREPTANTHUS ALBIDUS* Greene subsp. **peramoenus** (Greene) Kruckeberg hoc loc. *S. peramoenus* Greene, Bull. Torrey Club 13:142. 1886. Type: *Bolander*, in Oakland Hills.

Sepals lilac-lavender. Plants tending to be less robust than subsp. *albidus*.  $n = 14$ .

Specimens seen. Alameda County: Oakland Hills, *Michener & Bioletti* 672 (WTU) (5). Contra Costa County: 2 miles outside the north entrance to Mount Diablo State Park, *Morrison* and *Constance* 3030 (UC) (7). Santa Clara County: 0.3 miles southwest of Madrone, *Belshaw* 16167 (UC) (2).

Range and Variation of Species. *Streptanthus albidus* occurs on serpentine and ecologically similar sites in Alameda, Contra Costa and Santa Clara counties. Its robustness, the glabrous and glaucous herbage, combined with the flower color are its marks of distinction. It is here taken to include two distinct color variants. The lilac-lavender flowered subsp. *peramoenus* is found in the Oakland-Berkeley Hills, Mount Diablo, the hills above Sunol and the ridges of western Santa Clara County (e.g., upper Stevens Creek). Subspecies *albidus*, with greenish-white flowers is confined to the serpentine foothills south and east of San Jose around Coyote and Madrone. The two subspecies are fully interfertile and yet both are genetically isolated from all other members of the *S. glandulosus* complex.

3. *STREPTANTHUS NIGER* Greene, Bull. Torrey Club 13:141. 1886. *Euclisia nigra*, Leaflet. Bot. Obs. 1:83. 1904. Type: *Greene*, Point Tiburon, 1886.

General habit of *S. glandulosus*; herbage glabrous, glaucous-green throughout; plants simple or branched above the base, 2–8 dm. high; basal leaves lanceolate in outline, pinnately lobed, 5–7 cm. long; inflorescence open, the rachis “zig-zag”; pedicels 1.4–2.0 cm. long, twice as long as the flowers; sepals purplish-black with a distinct metallic cast, 0.7 cm. long; calyx appearing inflated, umbilicate based, the sepals strongly carinate; petals linear, the margins white and crisped, the median portion of the lamina veined purplish-black, exserted only 2–3 mm., barely reflexed; filaments of the upper pair of stamens connate almost throughout, their anthers wholly sterile; lateral and lower pairs of stamens barely exserted, crowded in the contracted throat of the corolla, through which the flat capitate stigma is forced; siliques stiffly ascending, straight, 5–6 cm. long; seeds oblong to oval, narrowly winged, 1.6–1.8 mm. long.  $n = 14$ .

Range and Variation. *Streptanthus niger* has never been found elsewhere than the type locality, on the southern tip of Tiburon Peninsula, Marin County, an area of not more than a square mile in extent. The plant is found in draws, slopes and ridges of the hilly area of the peninsula just above the narrow Raccoon Straits between the peninsula and Angel Island. The entire area is of stony, shallow soil derived from serpentine rock, and apart from the wholly barren spots, supports a varied and rather dense herbaceous vegetation, with only a very few and widely separated specimens of stunted *Umbellularia* and *Quercus*. The single population of *S. niger* is made up of small, semi-isolated colonies, with no apparent variation within or between colonies. It may well be, then, one of the most narrowly restricted species in the Californian flora.

As shown in figure one, hybrids between *S. niger* and any other member of the complex have been sterile. Thus, genetic isolation is complete between *S. niger* and even the most likely relatives of the species such as *S. glandulosus* subsp. *pulchellus* which grows on nearby Mount Tamalpais, or *S. albidus* subsp. *peramoenus* which occurs in the Berkeley Hills just across San Francisco Bay.

Specimens seen. Marin County: Rocky serpentine soil, Tiburon, *Raven* 843 (UC) (6).

Close relationship between the *S. glandulosus* complex and other streptanthi may be sought among other members of the section *Euclisia*, particularly the so-called “color-spot” species, aptly delimited by Morrison (1941) as the subsection *Insignes* (in his unpublished thesis). Hybrids between one of the *Insignes* group (*S. insignis* Jeps.) and *S. albidus* were quite fertile. *S. hispidus* Gray, another member of the *Insignes* group, appears to be related to *S. glandulosus* subsp. *pulchellus*. The author intends to expand the interfertility studies in *Streptanthus* to include other species of the genus, especially those in the section *Euclisia*.

ACKNOWLEDGEMENTS.—The author wishes to express his gratitude to two *Streptanthus* specialists, Mr. Freed W. Hoffman and Dr. John L. Morrison, for their continued advice and criticisms. Dr. C. Leo Hitchcock kindly read the manuscript. Thanks are due also to the curatorial staffs of the University of California and the United States National Herbarium for loans of specimens.

Department of Botany  
University of Washington  
Seattle 5, Washington

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## STUDIES OF THE POLLEN GRAIN AND POLLEN TUBE IN CERTAIN MALVACEAE

R. M. DATTA

The pollen grains of all Malvaceae in which they have been studied are round with spinescent outgrowths of varying shapes and lengths distributed uniformly on the exine wall (Wodehouse, 1935; Zander, 1935; Lang, 1937; Erdtman, 1952). A varying number of roundish conspicuous apertures is distributed evenly upon the exine surface. Concerning these apertures, Wodehouse (1935) remarks, "Though their shape and their function of serving as places of exit for the pollen tube prompt us to call them germ pores, there is much evidence to show that such apertures are morphologically furrows, which have become so shortened that they coincide in extent with their enclosed germ pores."

Amici (1830), the discoverer of the pollen tube, recorded polysiphonous germination of the pollen grain in *Hibiscus Trionum* and *H. syriacus*; in the latter species, some grains gave rise to twenty to thirty tubes. Guignard (1904) corroborated him after *in vivo* studies of *H. Trionum*, and found that only one tube plays a part in fertilization. Stenar (1925) found

in *Althaea rosea* ten tubes per grain, and in *Malva neglecta*, fourteen. Lang (1937) found five to ten tubes per grain produced by *Anoda cristata* and *Lavatera cachmeriana*, *in vitro*. Iyenger (1938) reported two tubes per grain in diploid Asiatic cotton (*Gossypium herbaceum*) and in tetraploid American cotton (*G. hirsutum*). He concluded that the frequency of two tubes is greater in the tetraploid American types than in the diploid Asiatic ones, and noted branching of the tubes, in the styles only. He noted polysiphonous germination also in *Hibiscus vitifolius*. Purewall and Randhawa (1947) found pollen grains of *H. esculentus* to germinate thirty minutes after they were placed in culture media. They grew more rapidly in culture media than under moist conditions. As many as six tubes were produced from some grains; branching of the tubes occurred both in culture media and on stigmatic surfaces.

The purpose of the studies here reported was to confirm and extend the foregoing observations.

#### ACKNOWLEDGMENTS

Grateful thanks are offered to Mr. K. N. Agha, Secretary, Indian Central Jute Committee, Calcutta, for kindly permitting this work to be carried on in the Jute Agricultural Research Institute, Nilganj, near Barrackpore, 24 Parganas, and to Dr. G. I. Patel, Cytogeneticist of the Institute, for his interest and for making facilities available. I am also obliged to Dr. P. K. Sen, Khaira Professor of Agriculture and Head of the Department of Agriculture, Calcutta University, for giving permission and facilities to complete the studies.

#### MATERIALS AND METHODS

The seventeen species, varieties, or races, upon which studies were made, are listed in Table 1.

A medium for *in vitro* studies was prepared as follows: 0.5 g. powdered agar agar and 1.0 g. sucrose were dissolved in 25 cc. boiling water. After cooling to 35°C., 0.5 g. powdered gelatin was added and dissolved by stirring. The mixture was filtered through muslin into test tubes plugged with cotton and was sterilized by suspending the tubes in boiling water for several minutes.

Drops of this medium were smeared on clean slides by the technique used in making blood films. The slides were dusted with pollen grains from flowers immediately after anthesis and placed in moist chambers consisting of large Petri dishes.

For *in vivo* studies, flowers were emasculated and bagged. On the following morning they were pollinated from fresh flowers of the same species. After 30–45 minutes, the styles were fixed in acetic-alcohol (1:1). On the following day they were transferred for storage to 70 per cent alcohol. When they were to be examined, they were boiled briefly in lactophenol, cooled, stained for 5 minutes in 1 per cent acid fuchsin, and squashed on the slides.

Studies of the sterility of pollen of *Hibiscus cannabinus* (the American race), *H. radiatus*, and *H. Sabdariffa*, were made late in November of 1954, when the two former species were near the end of their flowering season. Temporary mounts of the pollen of each species were made in aceto-carmine. Stained and unstained grains were counted. The diameters of fifty grains of each species were determined.

#### OBSERVATIONS

When one or more tubes grow forth from a grain, they contain at first hyaline cytoplasm which shows rapid circulatory movement. Afterwards, starch granules start flowing out of the pollen grain, gradually and ultimately packing up the pollen tubes, with their branches and ramifications, if present and making them turgid. When stained with iodine-potassium-iodide solution, the tubes become deep blue in color.

The tube nucleus and the generative cell or sperms are found in only one tube from a particular grain. As in the generality of pollen tubes, the tube nucleus lies nearer the tip than the generative cell. The generative cell follows the contour of the tube, but the tube nucleus sometimes bulges out slightly. Germination within the anther loculi, which has been observed in the tiliaceous genus *Corchorus* by Datta, 1956, has not been observed in Malvaceae.

Our observations on the occurrence of multiple and branching pollen tubes are given in Table 1.

The pollen grains of *Abutilon Theophrasti*, *Urena lobata*, and *Althaea rosea* failed to germinate under the conditions provided; those of *Abutilon Avicennae* germinated *in vitro*, but not within one half hour on the stigmas. In *Hibiscus esculentus*, germination was notably rapid, occurring *in vitro* within about five minutes at any period of the day; this shows that the grains remain viable throughout the day; and growth of the tubes was so rapid as to be easily perceived with the low power of the microscope.

Germination through more than one aperture was observed in every species in which germination took place, with the exception of *Malachra capitata*.

Branched pollen tubes were observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa*, *H. populneus*, *H. cannabinus* (the Indian, Ibadan, and Nigerian races, but not the American) and in  $F_1$  hybrids of *Hibiscus radiatus* and *H. cannabinus*. They were not observed in any of the other species. Since *Hibiscus cannabinus* (Indian) shows branching of the pollen tubes while *H. radiatus* does not, the appearance of this character in the hybrid suggests that it may be dominant.

Pollen of *Hibiscus radiatus* and *H. cannabinus* collected near the end of their period of flowering showed a low percentage of fertility, while *H. Sabdariffa*, still in full flower, was producing pollen of high fertility (Table 2). Ferguson (1924) and Kostoff (1932) have found the age of flowers to affect the fertility of pollen.

TABLE 1. Observations of germination of pollen grains, and of multiple and branching pollen tubes in certain Malvaceae, with references to the illustrations.

Species	Largest number of tubes observed from one grain		Branching	Illustrations
	<i>in vitro</i>	<i>in vivo</i>		
<i>Hibiscus vitifolius</i>	11	6	rare	Figs. 8, 9
<i>H. esculentus</i>	26	12	profuse	Figs. 1, 2, 3
<i>H. Sabdariffa</i>	9	8	frequent	Fig. 4
var. <i>altissima</i>	3		none	
<i>H. radiatus</i>	6		none	
<i>H. populneus</i> ( <i>Thespesia populnea</i> )	5		rare	
<i>H. cannabinus</i> (Indian)	11	17	slight	Figs. 5, 6, 7
<i>H. cannabinus</i> (Ibadan)	9		rare	
<i>H. cannabinus</i> (Nigeria)	5		rare	
<i>H. cannabinus</i> (American)	8		none	
<i>H. radiatus</i> × <i>H. cannabinus</i> (F <sub>1</sub> plants)	4		rare	Fig. 12
<i>Abutilon Avicennae</i>	3	no germination	none	
<i>A. Theophrasti</i>	no germination	no germination	none	
<i>Sida rhombifolia</i>	2	2	none	Fig. 10
<i>Malachra capitata</i>	1	2	none	Fig. 11
<i>Urena lobata</i>	no germination	no germination		
<i>Althaea rosea</i>	no germination	no germination		

The average diameter of pollen grains of *H. Sabdariffa* as we have determined it, namely 127.9 $\mu$ , is distinctly smaller than as reported by Lang (1937), namely 145.5 $\mu$ .

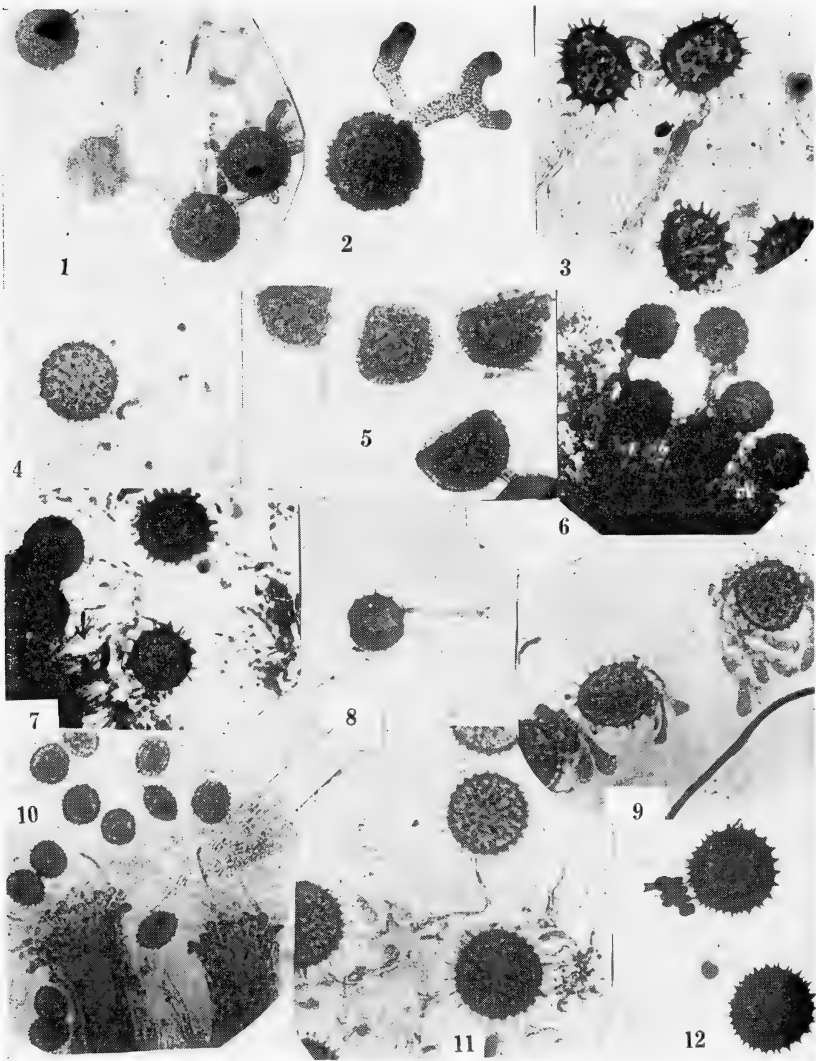
TABLE 2. Observations of fertility and dimensions of pollen grains of three species of *Hibiscus*.

Species	Number of pollen grains examined	Number of stained grains	Number of non-stained grains	Percentage sterility	Range of diameters	Average diameter of 50 grains
<i>H. radiatus</i>	383	179	204	53.26	98.4–139.4 $\mu$	120.96 $\mu$
<i>H. cannabinus</i>	450	163	287	63.76	131.12–188.6 $\mu$	153.5 $\mu$
<i>H. Sabdariffa</i>	396	353	43	10.86	98.4–147.6 $\mu$	127.9 $\mu$

## SUMMARY

Production of pollen tubes from more than one aperture of the pollen grain has been observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa* and its variety *altissima*, *H. radiatus*, *H. populneus*, *H. cannabinus*, first generation hybrids of *H. cannabinus* and *H. radiatus*, *Abutilon Avicennae*, and *Sida rhombifolia*.





Figs. 1-12. Germination of pollen of Malvaceae: 1, 2, *Hibiscus esculentus* in vitro; 3, *H. esculentus* in vivo; 4, *H. Sabdariffa* in vivo; 5, *H. cannabinus* (Indian) in vitro; 6, 7, *H. cannabinus* (Indian) in vivo; 8, *H. vitifolius* in vitro; 9, *H. vitifolius* in vivo; 10, *Sida rhombifolia* in vivo; 11, *Malachra capitata* in vivo; 12, F<sub>1</sub> hybrid of *H. radiatus* × *H. cannabinus* in vitro.

Branched pollen tubes have been observed in *Hibiscus vitifolius*, *H. esculentus*, *H. Sabdariffa*, *H. populneus*, *H. cannabinus* (Indian, Ibadan, and Nigerian races), and first generation hybrids of *H. cannabinus* and *H. radiatus*.

Low fertility of pollen observed in *H. cannabinus* and *H. radiatus* is believed to have been caused by lateness of season.

Department of Agriculture,  
Calcutta University

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#### A NEW SPECIES AND SOME NOMENCLATURAL CHANGES IN *Solanum*, SECTION TUBERARIUM

DONOVAN S. CORRELL

In 1852, Dunal described *Solanum lycopersicoides*, no named because of its close resemblance to some of the species in the genus *Lycopersicon*, the common garden tomato. Sometime between 1909 and 1914, Weberbauer collected a plant in an undesignated locality in Peru which, though quite different, superficially resembled *Solanum lycopersicoides*. Again, in 1925 Pennell obtained the same plant at Quive in the Department of Lima.<sup>1</sup> Until now, no apparent attempt was ever made to identify these collections. This distinctive plant is here named in honor of the latter

<sup>1</sup> Since preparing this manuscript, Earl E. Smith, Ramón Ferreyra and I found a solitary sterile plant above Canta in the Department of Lima, Peru, on March 7, 1958.

collector, an unassuming and scholarly gentleman who will long be remembered for his work on the family Scrophulariaceae.

These two species belong to Series *Juglandifolia* in Subsection *Hyperbasarthrum* of Section *Tuberarium*, characterized by being somewhat woody non-tuber-bearing plants with yellow stellate or rotate-stellate corollas, and pedicels that are articulate above the very base. Because these two species appear to stand alone as the closest links between *Solanum* and *Lycopersicon*, they are both here treated for convenience in comparing their individual characteristics.

Leaflets suborbicular, coarsely crenate; pedicels articulate well below the middle or near the base ..... *S. pennellii*

Leaflets irregularly pinnatifid; pedicels articulate less than 3 mm. below the calyx. .... *S. lycopersicoides*

***Solanum pennellii*** sp. nov. Herba habitu *S. lycopersicoidei* similis, omnino glanduloso-pubescent, ramosa; folia imparipinnata; foliola petiolulata, suborbicularia, crasse crenata, basi truncata vel cordata; inflorescentia terminalis vel ramos laterales terminans, corymbosa vel racemosa; pedunculus bracteis singulis vel pluribus semiorbicularibus aliquando in inflorescentiam procurrentibus ornatus; pedicelli multo infra medium vel prope basim articulati; flores flavi vel lutei; corolla lobis late ovatis, acutis vel subobtusis rotato-stellata; antherae diadelphicae, supra medium valde curvatae; stylus pilis longis sericeis ornatus, prope apicem valde curvatus; ovarium globosum.

Plant woody-herbaceous, erect, 5 dm. or more tall, glandular-pubescent throughout, rootstock unknown but doubtless non-tuber-bearing; stem woody; leaves odd-pinnate, up to 13 cm. long, with few interstitial leaflets, the leaflets 5 or 7, prominently petiolulate, suborbicular, coarsely crenate, truncate to cordate at base, up to 4 cm. in diameter; petiolules up to 1 cm. long; pseudostipular leaves shaped similarly to the leaflets but somewhat reniform, 1–2 cm. long; inflorescence terminal or terminating the lateral branches, corymbose or racemose, few- to many-flowered; peduncle slender, up to 8 cm. long, provided with one or more semiorbicular bracts that sometimes continue into the inflorescence; pedicels slender, up to 2 cm. long, articulate well below the middle or near the base; flowers lemon-chrome; calyx 5–6 mm. long, divided to near the base into oblong-elliptic obtuse lobes; corolla rotate-stellate, up to 3.5 cm. in diameter, the lobes broadly ovate and acute to subobtuse; anthers of two lengths, linear-oblong in outline, the largest up to 10 mm. long, the smaller up to 7 mm. long, strongly recurved above the middle, opening by two pores at the apex that soon become slit to the base of the anthers, the filaments rather thick, up to 2 mm. long; style up to 11 mm. long, strongly curved near the apex, adorned with long silky hairs for most of its length; stigma elongate and prominent; ovary orbicular; fruit unknown but probably orbicular.

Specimens examined. PERU. Department of Lima, Quive, open rocky

slope, herb, corolla "lemon chrome," alt. 800–1000 m. ("plant ascending to 2500 m."), June 9, 1925, *F. W. Pennell 14304* (type, PH, sheet no. 642829); Peru, 1909–1914, *Weberbauer 5315* (without other data) (F, no. 627894); Peru, hanging from cut along road above Canta, Department of Lima, 2,850 m. alt., plant branching from a woody rootstock, no flowers or fruits present, March 7, 1958, *Correll, Smith & Ferreyra P287* (LUNDELL).

*SOLANUM LYCOPERSICOIDES* Dunal in DC. Prodrumus 13 (1):38. 1852; Bitter, Repert. Sp. Nov. 11:466. 1912; Ochoa, "Agronomia" 18 (74): 13–16. 1953.

Plant bushy, glandular-pubescent throughout, up to 2.5 m. tall, non-tuber-bearing; stem woody, erect or tortuously ascending; leaves asymmetrically pinnate-pinnatifid, up to 13 cm. long, with numerous toothed interstitial leaflets, the leaflets 7 to 11, sessile to decurrent on the rachis or rarely shortly petiolulate, irregularly pinnatifid, up to 5 cm. long, with the pinnules often toothed and the ultimate segments obtuse to acute; pseudostipular leaves lobed similarly to the leaflets, about 1 cm. long; inflorescence terminal, subterminal or terminal on the branches, corymbose, many-flowered; peduncle rather stout, 4–9 cm. long; pedicels slender, up to 12 mm. long, articulate 1–2 mm. below the calyx; flowers bright yellow, showy; calyx 3.5–5.5 mm. long, divided to about the middle into ovate to ovate-lanceolate acute to acuminate lobes; corolla rotate-stellate, about 2 cm. in diameter, with short triangular lobes, coarsely pubescent on the outer surface; anthers 3.5–5 mm. long, oblong-elliptic in outline, opening by two large pores at the apex that commonly become longitudinal slits on the inner surface extending from apex to base, the filaments filiform, 1–2 mm. long; style 7–12 mm. long, slender, pubescent below, with a conspicuously clavellate stigma; fruit orbicular, about 6 mm. in diameter, purple-black, marked with green.

Specimens examined. PERU. Department of Tacna: Cordillera de Palca, *A. D'Orbigny 291* (type collection, P, MPU); Cordillera de Palca, 1851, *Weddell* (P); Quebrada de Palca, *von Tschudi* (W); Prov. Tarata, open hillside among lava boulders, alt. 2900 m., bush 2–2.5 m. high, calyx yellow-green, corolla bright yellow, fruit purple-black and green at base, April 25, 1942, *Metcalfe 30404* (G, MO, US); Prov. Tarata, near Candarave, dry open hillside, in clay soil and volcanic rock, 2800 m. alt., bush 0.7–2 m. tall, calyx green, corolla yellow, fruit green and black at base, April 15–25, 1942, *Metcalfe 30382* (G, MO, US); Causiri, a un kilómetro mas arriba de Palca y a 45 klmts. de Tacna, March 20, 1953, *Ochoa 2035* (GH, US).

Although these two species are closely allied, they differ from each other in the shape of their leaflets as well as in their floral characters. The sub-basal articulation of the pedicels of *S. pennellii* in contrast to the sub-apical articulation of those of *S. lycopersicoides* is distinctive. Although the anthers of both species eventually split to the base at anthesis, those of *S. pennellii* have at first prominently marginate terminal pores while



FIG. 1. Solanum. A. *Solanum lycopersicoides*, upper part of plant, D'Orbigny 291;  
B. *Solanum pennellii*, upper part of plant, Weberbauer 5315.

the anthers of *S. lycopersicoides* appear never to have well defined terminal pores. In fact, many of the species in Section *Tuberarium* have anthers that are split to the base, although this process may be considerably delayed. The weak tissue below the apical pores is frequently easily ruptured.

These two species are living evidence in support of those who would combine *Solanum* and *Lycopersicon*. They are true representatives of a transition between these two genera. The lack of an apical sterile tip to the anthers, however, traditionally place them in *Solanum*, although the anthers of both are commonly split their entire length as in *Lycopersicon* and both closely resemble in habit some of the species in that genus. Furthermore, Rick (in Proc. Nat. Acad. Sci. 37 (11):741-744. 1951) has demonstrated that *Solanum lycopersicoides* can be hybridized with *Lycopersicon esculentum* Mill.

***Solanum hougassii*** Correll nom. nov. *Solanum verrucosum* Schlecht. var. *spectabilis* Correll, U. S. Dept. Agr., Agr. Monogr. No. 11:228, figs. 164-166. 1952. *Solanum spectabile* (Corr.) Hawkes, Ann. and Mag. Nat. Hist., ser. 12, vol. 7:701. September, 1954; Swaminathan and Hougass, Am. Jour. Bot. 41:650. October, 1954 (as *S. spectabilis*), non *S. spectabile* Steudel, Nomenclator Botanicus, ed. 2, pt. 2:606. 1841.

The above authors, Hawkes, Swaminathan and Hougass, independently came to the same conclusion regarding the proper status of this plant. Apparently sensing a need for urgency, they published their results within a month of one another. Unfortunately, in elevating the variety to a specific category a homonym resulted. It is a pleasure to rename this Mexican species for R. W. Hougass, the able and congenial project leader for the Inter-regional Potato Introduction and Preservation Project at Sturgeon Bay, Wisconsin.

***Solanum nelsonii*** Correll nom. nov. *Solanum confusum* Correll, U. S. Dept. Agr., Agr. Monogr. No. 11:63, figs. 41-42. 1952, non *S. confusum* Morton, Contr. U. S. Nat. Herb. 29:70. 1944.

At the time of publishing my work on *Solanum* in 1952, the Gray Index to which I referred was, unknowingly to me, not up to date. This accounts for the publication of this homonym. This species, a native of Oaxaca, Mexico, is here renamed in honor of E. W. Nelson who collected the type specimen.

The author, who is in the process of classifying and coordinating all data regarding the species in the Section *Tuberarium* of *Solanum*, is indebted to the Agricultural Research Service, United States Department of Agriculture and National Science Foundation, as well as to Texas Research Foundation, for continuous support and encouragement in the pursuance of this difficult problem, of which this is a part.

Texas Research Foundation,  
Renner, Texas

## DOCUMENTED CHROMOSOME NUMBERS OF PLANTS

(See Madroño 9: 257-258. 1948)

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
POLYGONACEAE				
<i>Eriogonum inflatum</i> Torr. & Gray	n = 16	D. Stone & P. Raven UC <sup>1</sup>	Raven 10850 UC	Road to Panoche, San Benito County, Calif.
SCROPHULARIACEAE				
<i>Castilleja breviloba</i> 'a Piper	n = 12	L. R. Heckard ILL	Heckard 267 JEPS	Northeast of Gasquet, Del Norte County, Calif.
<i>chromosa</i> A. Nels.	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4252 JEPS	Northwest of Baldwin Lake, San Bernardino Mts., San Bernardino County, Calif.
<i>*inflata</i> Pennell	n = 36	L. R. Heckard ILL	Heckard 800 JEPS	Point Reyes light-house, Marin County, Calif.
<i>integra</i> A. Gray	n = 12	L. R. Heckard ILL	P. C. Silva, 29 Aug. 1955 JEPS	19 miles east of Springerville, Apache County, Ariz.
<i>linariaefolia</i> . Benth.	n = 12	L. R. Heckard ILL	Mason 14563 JEPS	East of Campito Mt., White Mts., Mono County, Calif.
<i>pilosa</i> S. Wats.) Rydb.	n = 12	L. R. Heckard ILL	Bacigalupi 4295 JEPS	Franktown, Washoe County, Nev.
<i>roseana</i> Eastw.	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4052, 4053 JEPS	City Creek Canyon, San Bernardino Mts., San Bernardino County, Calif.
<i>roseana</i> Eastw.	n = 12	L. R. Heckard ILL	Heckard 493 JEPS	Lewis Creek Road, Monterey County, Calif.
<i>stenantha</i> A. Gray	n = 12	L. R. Heckard ILL	Bacigalupi (& Heckard) 4085 JEPS	Potrero Creek, near Barrett Junction, San Diego County, Calif.
COMPOSITAE				
<i>Bidens laevis</i> (L.) B. S. P.	n = 11	A. M. Torres UNM	Torres 52 UNM	Bernalillo County, New Mexico
<i>Borrchia arborescens</i> (L.) DC.	2n = 28	R. T. Neher IND	Heiser 3195 IND	Dade County, Florida

\* Prepared slide available.

<sup>1</sup> Symbols for institutions are those listed by Lanjouw and Stafleu, Index Herbariorum, Part I. Third Edition, 1956, Utrecht.

SPECIES	NUMBER	COUNTED BY	COLLECTION	LOCALITY
<i>frutescens</i> (L.) DC.	2n = 28	R. T. Neher IND	Heiser 3205 IND	Manatee County, Florida
<i>Simsia</i> <i>grandiflora</i> Benth.	n = 17	C. B. Heiser IND	Heiser R7 IND	San Salvador, Salvador
<i>polycephala</i> Benth.	n = 17	C. B. Heiser IND	Heiser R5 IND	Antigua, Guatemala
<i>Thelesperma</i> <i>intermedium</i> Rydb.	n = 8	A. M. Torres UNM	Torres 12 UNM	Bernalillo County, New Mexico
<i>longipes</i> Gray	n = 10	A. M. Torres UNM	Torres 18 UNM	Otero County, New Mexico
<i>megapotamicum</i> (Spreng.) Kuntze	n = 11	A. M. Torres UNM	Torres 10 UNM	Socorro County, New Mexico
<i>subnudum</i> Gray	n = 12	A. M. Torres UNM	Torres 23 UNM	San Juan County, New Mexico

## APOMIXIS IN THE GRAMINEAE. TRIBE ANDROPOGONEAE: HETEROPOGON CONTORTUS

W. H. P. EMERY AND W. V. BROWN

*Heteropogon contortus* (L.) Beauv. ex Roem. & Schult. consists of a relatively uniform series of populations with an extensive native range throughout most of the tropical and sub-tropical grassland regions of the world. In parts of the Hawaiian Islands, Australia, Indo-Malaya, India, Asia Minor, Africa, Europe, and the Americas it forms an important part of the range forage. The species is both palatable and nutritious, but when mature the plants produce fertile spikelets which have a sharply pointed callus and a stout hairy awn. These spikelets may penetrate the skin or lining of the digestive tract (Pammel, 1911), causing severe irritation and infection. They may even affect the general health of grazing animals (Chippindall, 1954).

Previous cytological studies of *H. contortus* from various parts of the world have shown that many of the populations which comprise this species are characterized by highly irregular meiotic divisions. Gould (1956) reported that some irregularities were observed in meiotic divisions of the pollen mother cells (PMC's) in six collections from Texas and northern Mexico. Mehra (1954) examined six collections from India and reported varying numbers of univalent, bivalent, trivalent, and quadrivalent configurations in the microsporocytes of each collection. On the other hand, Celarier and Harlan (1953) examined collections from Tanganyika, India, Australia, and Madagascar and noted a high degree of irregularity in the



PMC's of the first three, but an almost regular division in the PMC's of the collection from Madagascar.

Evidence for the existence within the species of a polyploid series, with occasional aneuploid forms, appears well-substantiated by a number of workers (Brown, 1951; Celarier and Harlan, 1954; Darlington and Janaki-Ammal, 1946; de Wet, 1956; Gould, 1956; and Mehra, 1954). The chromosome counts reported in 22 different collections of *H. contortus* range from  $2n=20$  to  $2n=80$ , with modes at  $2n=40$  and  $2n=60$ . The irregularity of meiotic divisions, and the existence of an extensive polyploid series of chromosome forms, suggested the possibility of apomixis in this species.

MATERIALS AND METHODS

Seed from thirty collections were obtained through the generous cooperation of Dr. R. P. Celarier of the Oklahoma Agricultural Experiment Station and Dr. E. J. Britten of the Hawaii Agricultural Experiment Station. Flowering material of twelve American collections was provided through the cooperation of Dr. F. W. Gould of Texas Agricultural and

TABLE 1. CULTURES OF HETEROPOGON CONTORTUS EXAMINED<sup>1</sup>

CULTURE NO.	PLACE OF ORIGIN	2n	CULTURE NO.	PLACE OF ORIGIN	2n
A-4595-1	Galton, Australia	....	A-3729-4	Southern Rhodesia	....
A-4595-3	Galton, Australia	....	A-3050-2	Madagascar	40
A-3962	Borgar, Java	40	A-3050-3	Madagascar	40
A-2667	New Delhi, India	40	G-683	Monterrey, Mexico	60
A-5293	Delhi, India	....	G-730	Durango, Mexico	...
A-5298	India	....	G-788	Parral, Mexico	....
A-2668	Coimbatore, India	40	G-847	Chihuahua, Mexico	60
A-3230-3	Allahabad, India	40	G-420	Cuauhtemoc, Mexico	....
A-4829	Dehra Dun, India	....	G-384	Chihuahua, Mexico	60
A-3703-1	Belgian Congo	40	G-500	Durango, Mexico	....
A-3703-2	Belgian Congo	40	G-1485	Durango, Mexico	....
A-3703-3	Belgian Congo	40	G-1556	Coahuila, Mexico	....
A-3234	Kenya	40	G-874	Encino, Texas	....
A-3729-1	Southern Rhodesia	....	G-873	Encino, Texas	....
A-3729-3	Southern Rhodesia	....	.....	Artesia Wells, Texas	....
			.....	Marathon, Texas	....

<sup>1</sup> Voucher specimens for all collections utilized in this study will be deposited in the University of Texas Herbarium. Collections bearing the prefix "A" are also deposited in the Oklahoma State University Herbarium, Stillwater, Oklahoma, and were obtained through the cooperation of that institution. Those with the prefix "G" were provided by the Texas Agricultural and Mechanical College. The plants from Artesia Wells and Marathon, Texas, are collections of the authors.

Mechanical College. The authors wish to express their thanks to these men, as well as to all others who were instrumental in assembling seed from the foreign collections of this species.

Plants of fifteen non-American cultures (7 Indian, 4 African, 1 from Madagascar, 2 Australian, and 1 from Java) were established in our grass nursery together with two collections from Texas.

Collections utilized in the embryological examination of *H. contortus*, together with their place of origin, are given in Table 1. Flowering material at various stages of development was killed and fixed in Navashin's fluid. Pistils were dissected from the florets, dehydrated in butyl-ethyl alcohol, embedded in Tissuemat, sectioned at 8 to 12 microns, and stained in Delafield's hematoxylin.

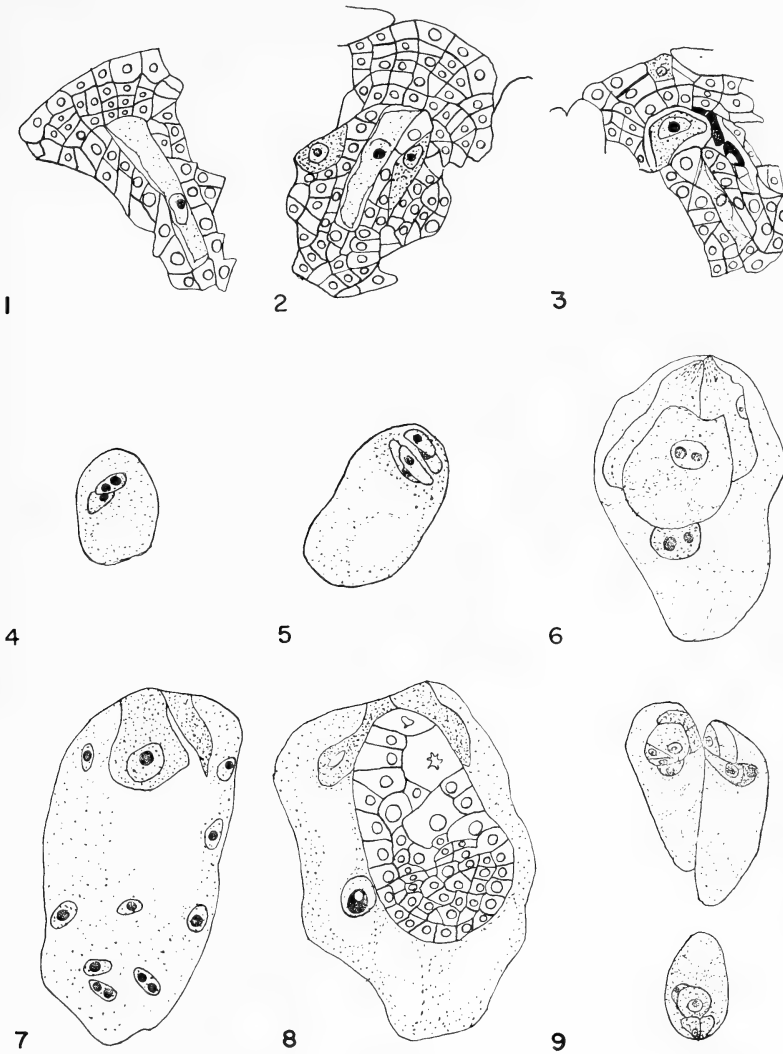
#### OBSERVATIONS

All thirty-one plants from twenty-five different collections of *H. contortus* examined in this study were found to be aposporous apomicts. The apomictic mechanism involves the regular degeneration of the egg mother cell (EMC) (figs. 1, 2) not later than early prophase of meiosis, and the simultaneous or subsequent development of aposporous embryo sac initials (figs. 2, 3). No EMC division nor derivatives from such a division were observed in this study. The degeneration of the EMC appears to be dependent on factors inherent within the cell, since in many ovules degeneration occurs even in the absence of aposporous embryo sac initials (fig. 1). The EMC becomes less turgid, the cytoplasm becomes more granular and lighter staining. Finally the cell degenerates completely.

Following a period of enlargement and vacuolization, the nucleus of the aposporous embryo sac initial divides twice in rapid succession to produce four nuclei. These nuclei commonly remain in the micropylar end of the embryo sac (figs. 4, 5). As development of an embryo sac proceeds, the four nuclei usually organize into 4-nucleate, 4-celled embryo sacs, with 1 egg, 2 synergids, and 1 polar nucleus (fig. 6). Occasionally, however, 4-nucleate, 3-celled embryo sacs were observed containing 1 egg, 1 synergid, and 2 polar nuclei. No 8-nucleate embryo sacs were observed in the present material.

Many ovules of *H. contortus* produce only one aposporous embryo sac. In a majority of the ovules, however, two or more aposporous embryo sacs commonly develop. These embryo sacs appear to compete for the available space or nutritive supply, enlarging and encroaching upon each other as they develop.

The development of the embryo and endosperm begins shortly after, but apparently never prior to, anthesis. It was not determined if pollination is a prerequisite to development, but the appearance of pollen tube remnants in embryo sacs shortly after anthesis together with the subsequent development of embryos and endosperm strongly suggests that *H. contortus* is pseudogamous. Commonly the endosperm undergoes a num-



FIGS. 1-9. *Heteropogon contortus* (figs. 1-3, 6-9,  $\times 300$ ; fig. 4  $\times 440$  and fig. 5,  $\times 100$ ): 1, egg mother cell (EMC) starting to degenerate; 2, partially degenerate EMC and two developing aposporous embryo sac initials; 3, developing aposporous embryo sac initial at the apex of the nucellus and a portion of the degenerating EMC; 4, two-nucleate aposporous embryo sac with both nuclei in one end of the embryo sac; 5, the four-nucleate aposporous embryo sac; 6, a four-nucleate aposporous embryo sac organized with one egg, two synergids, and a single polar nucleus; 7, embryo sac showing the early development of endosperm prior to the initial division of the unreduced egg cell; 8, several-celled embryo and an undivided polar nucleus; 9, three aposporous embryo sacs of the same ovule showing development of a small mature four-nucleate sac in the chalazal region separated from the other two by several layers of nucellar tissue.

ber of divisions before the initial transverse division of the unreduced egg cell (fig. 7), but this pattern of development varies even within different ovules of the same inflorescence. Not infrequently embryos of 32–64 cells were observed “capped” at their apex by an undivided crescent-shaped, polar nucleus (fig. 8).

Although a majority of the aposporous embryo sacs develop in contact and later encroach upon one another, occasional ovules with multiple embryo sacs were observed in which the developing aposporous embryo sacs are relatively small, are separated by nucellar tissue, and develop to maturity without being encroached upon by other embryo sacs of the ovule (fig. 9).

The apomictic mechanism in *H. contortus* is one involving the regular production of 4-nucleate, aposporous embryo sacs followed by parthenogenesis. The complete failure of meiosis in megasporocytes of this species indicates that *H. contortus* is, or closely approaches, the condition of an obligate apomict.

#### DISCUSSION

*Heteropogon contortus* is another species in the rapidly increasing list of grasses known to reproduce in whole or in part by agamospermy. *Heteropogon contortus* seems to be essentially an obligate apomict throughout its range, forming 4-nucleate, aposporous embryo sacs followed by parthenogenesis. It is obvious that, although *H. contortus* seems to be essentially an obligate apomict, variation within the species does arise, possibly through occasional hybridization, polyploidy, or chromosome loss. The occurrence of various chromosome forms, together with univalent and multivalent chromosome configurations in the microsporocytes, tends to indicate the probability of some intra- or inter-specific hybridization at one or more periods during the existence of the taxon. The possibility of sexual recombination during recent times is further suggested by the existence of diploid plants of *H. contortus* in India (Janaki-Ammal, 1946). Diploid relatives of aposporous apomicts are almost without exception sexual (Gustafsson, 1947).

The presence of diploid *H. contortus* in India, the fact that most Old World plants of the species have  $2n = 40$  and  $2n = 60$ , and that all New World plants have  $2n = 60$  or above would indicate that southern Asia might be the center of origin of the species. Southern Asia is considered to be the center of origin of the tribe Andropogoneae (Hartley, 1950). An Old World origin for the tribe is further indicated by the existence of numerous genera in the Old World that do not occur in the New, whereas there are no genera of New World Andropogoneae not present also in the Old World.

In most details the apomictic process in *H. contortus* is very similar to that reported by the authors (Brown and Emery, 1957) in *Themeda triandra* and *Bothriochloa ischaemum* of the Andropogoneae. The process

is also similar to that reported in species from various genera of the Paniceae, i.e., *Cenchrus* (Snyder, 1955), *Panicum* (Warmke, 1954), *Paspalum* (Smith, 1948), *Pennisetum* (Narayan, 1951), *Setaria* and *Urochloa* (Emery, 1957).

In both tribes (except, perhaps, for *Tripsacum* and *Saccharum*) 4-nucleate aposporous embryo sacs are produced following the degeneration of the sporogenous tissue. Pseudogamy appears to be characteristic of all apomicts in these two tribes. A minor difference in the process as it occurs in the two tribes seems to be the time of degeneration of the sporogenous tissues. In the Paniceae degeneration occurs during or just following the formation of megaspores. In the Andropogoneae the megasporocyte degenerates not later than early prophase of meiosis.

There are a number of aposporous grasses in other tribes of the family, but the process in them differs significantly from that in species of the Andropogoneae and Paniceae. In *Bouteloua curtipendula* (Chlorideae) four megaspores are produced by a very irregular apomeiotic division. The chalazal spore enlarges somewhat before it, like the other three spores, degenerates. The aposporous embryo sac is 8-nucleate (Brayant, 1952). In aposporous *Poa* species (Festuceae) the megasporocyte may complete meiosis and may form a functional reduced embryo sac. Whenever aposporous embryo sac initials are formed, however, they inhibit to some extent further development of the megasporocyte or spores. The aposporous embryo sacs produced are usually 8-nucleate when, and if, they reach maturity (Nygren, 1950). As far as known, therefore, the regular formation of 4-nucleate aposporous embryo sacs is restricted to the apomictic species of the Paniceae and Andropogoneae.

*Heteropogon contortus* is one of the very few grasses supposedly native to both the Old and New World tropics. Although varying greatly in the frequency of occurrence, the distribution of *H. contortus* is reported from every major land mass between 35°N. latitude and 35°S. latitude, and so far as can be determined from existing botanical literature, it is endemic in the New World, and in the Old World from South Africa to Australia, and numerous islands of the Pacific Ocean. The similarity of the apomictic process in clones from different parts of the species range suggests a common origin of the apomictic mechanism previous to the spread of the species throughout its present pan-tropical distribution. The alternative possibility is that apospory has arisen two or more times in isolated populations of the species and subsequently has developed to the same stage in each.

It is interesting to speculate on the possible age of apomixis in *H. contortus* since here is a highly successful, essentially obligate apomictic species, capable of establishing itself in climax grasslands of many regions. Parallel evolution of identical mechanisms for reproduction in various discontinuous and completely isolated populations seems unlikely in such a morphologically uniform species, and thus it may be con-

cluded that the development of apomixis in this species predates its trans-oceanic distribution.

If the pantropical distribution of *H. contortus* occurred in recent times, then the development of the apomictic mechanism in this species may also be a recent occurrence. If, on the other hand, its distribution occurred together with other tropical and sub-tropical floras, then the development of the apomictic mechanism may date back to the end of the Eocene epoch or earlier. The latter possibility would imply a very old species that, in spite of essentially obligate asexual reproduction, has spread widely and survived despite competition with sexually reproducing species in a variety of environments. There is no documentary evidence known to the authors indicating post-Columbian transfer from the Old World to the New or vice versa. Nevertheless, *Heteropogon* is one of the most highly specialized genera of the Andropogoneae and has two pan-tropical species. It is possible that its highly specialized spikelets, with their sharply barbed callus, may have permitted a recent pre-Columbian intercontinental migration.

In his extensive treatise on apomixis, Gustafsson (1947, p. 303) points out that the phytogeographical data on a number of distinct apomictic micro-species of glaciated regions seems definitely to prove the Old-Quaternary age of such taxa, and therefore, that the condition of agamospermy itself must have arisen in even more remote times. Apomixis in these species has existed, therefore, for somewhat more than one million years. This is the oldest estimate on the age of apomixis in extant species known to the authors, although Clausen (1954) states, "The facultative apomicts have exploited an extremely effective solution to these contrasting demands (referring to environment and species variability), a solution that enables them to store interspecific variability and to nevertheless remain constant for ages."

It appears reasonable that if apomictic microspecies of *Taraxacum*, *Hieracium*, and *Alchemilla* (cited by Gustafsson, 1947) have existed since the late Tertiary in a region of considerable environmental instability, then a definite possibility exists that an essentially obligate apomictic species might have endured under the more stable tropical and sub-tropical environments for a much greater period of time. The duration of apomixis in *Heteropogon contortus* may be short or very long; for the present it remains in the realm of speculation.

#### SUMMARY

1. Cytological studies of *Heteropogon contortus* (L.) Beauv. ex Roem. and Schult., a perennial forage range grass with an extensive range throughout most of the tropical and sub-tropical grassland regions of the world, revealed this species to be an essentially obligate, aposporous apomict with probable pseudogamous development of embryos.

2. The apomictic mechanism, as studied in twenty-five collections from various parts of the Old and New worlds, involves the regular degenera-

tion of the egg mother cell, initiation of one to several aposporous embryo sac initials, and, following two nuclear divisions in each sac, the organization of 4-nucleate aposporous type embryo sacs, these commonly with one egg, two synergids, and a single polar nucleus. Development of the embryo is probably pseudogamous, but is not dependent on the prior development of endosperm.

3. The close parallel between the apomictic mechanisms of *H. contortus*, *Bothriochloa ischaemum*, and *Themeda triandra* of the Andropogoneae and the reproductive mechanisms of previously reported aposporous apomicts of the Paniceae is pointed out.

4. Parallel evolution of identical apomictic mechanisms for reproduction in various discontinuous populations seems unlikely, and the authors conclude that the age of apomixis in *H. contortus* predates its trans-oceanic distribution. If this distribution were recent, then the age of apomixis in the species may be recent; but if the species were distributed as part of a tropical or a sub-tropical flora, then the age of apomixis may date back to the end of the Eocene epoch or earlier.

The Grass Research Project  
Plant Research Institute  
The University of Texas, Austin, Texas

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IRIS, SECTION APOGON, SUBSECTION OREGONAE  
SUBSECT. NOV.<sup>1</sup>

QUENTIN D. CLARKSON

*Iris tenuis* Wats. is endemic to the upper Clackamas River and its tributary, Eagle Creek, in Clackamas County, northwest Oregon. A single specimen collected in 1884 from Washington County, Oregon, is apparently mislabeled, as the species has not been collected since from that area.

While the specific validity of *I. tenuis* has not been questioned, it has been included by authors in subsection *Californicae* of section *Apogon* only with some reluctance. Foster (1937) called attention to its morphological and cytological distinctions, but left it in the *Californicae*. Simonet (1934) placed the species in the *Sibiricae* mainly on cytological grounds, but Foster rejected this treatment for morphological reasons. Smith and Clarkson (1956) on the basis of cytological data proposed its removal from the *Californicae*.

Simonet reported a chromosome number of  $n=14$  for *I. tenuis*. Smith and Clarkson confirmed this number and also reported that fertile hybrids between other members of the *Californicae* are easily produced, but that hybrids could not be produced between *I. tenuis* and *I. tenax* Dougl. Presumably this barrier extends to other members of the subsection. Morphologically *I. tenuis* differs distinctively from other *Californicae* in having ensiform leaves and scarious instead of green bracts. Superficially, as Foster pointed out, it resembles *I. cristata* Ait., and the general appearance of the species is unlike other *Californicae*.

Inclusion with the *Sibiricae*, as proposed by Simonet, seems unwise not only because of morphological differences but also because of geographical considerations. If *I. tenuis* is placed with the *Sibiricae* it becomes an isolated member of the subsection with little in common except a possible base chromosome number of  $n=7$ .

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<sup>1</sup> Grateful acknowledgment is made to Sister John Mary of Marylhurst College for her assistance with the Latin diagnosis and to Dr. Helen Gilkey of Oregon State College for her helpful comments.



Regardless of origin, *I. tenuis* is sufficiently distinct, morphologically, cytologically, and geographically, to warrant erection of a new subsection which is accordingly proposed.

IRIS, sect. APOGON, subsect. **Oregonae**, subsect. nov. Perennes ex rhizomis gracilibus; folia ensiformia, subviridia, basibus scariosis, equitantes; caulis ramosus, 2–3 flores in omni ramo; spathae scariosae, oppositae, unifloriferae; perianthii tubus pedicellusque breves; flores pallide albi aut caeruleo-tincti.

Perennials from slender rhizomes; leaves ensiform, pale green, scarious at base, equitant; stems branched, 2–3 flowers on each branch; spathes scarious, opposite, 1-flowered; perianth tube and pedicel short; flowers pale white or tinged with blue. Type species. *I. tenuis* Wats. Proc. Amer. Acad. XVII: 380. 1882.

Division of Science  
Portland State College  
Portland, Oregon

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SMITH, FRANK H. and QUENTIN D. CLARKSON. 1956. Cytological studies of inter-specific hybridization in Iris, subsection Californicae. Am. Jour. Bot. 43:582–588.

#### REVIEWS

*How to Identify Plants.* By H. D. HARRINGTON. 203 pp., illustrated by L. W. Durrell. Sage Books. 1957. Denver, Colo. \$3.00.

This handy, pocket-sized "how-to-do-it" book, by the author of the Manual of the Plants of Colorado, is designed "to provide practical help for those interested in learning the special technique of identifying plants." It is printed by offset and has numerous, simple line drawings. The more common descriptive terms are grouped into eight chapters, each chapter devoted to a particular category of structure, e.g., flower, stem, leaves. The student is advised to commit these terms to memory, whereas terms less commonly used are included in a 79-page, partly illustrated glossary for reference, at the end of the book. Although the definitions are said to be based on usage in the "average manual," "cell" is eschewed for "locule," and one might wish that the term "pistil" had been avoided also, because it is difficult to homologize with the idea of sporophylls (page 29, fig. 46). A key is offered to the characters of leaf surface, and another to common types of fruit; in the latter the use of both "pistil" and "carpel" seems needlessly confusing. A special chapter on the use of keys, including synoptical, bracket, and indented types, contains useful comments on difficulties likely to be encountered and means of overcoming them. Collecting and preparing specimens are described succinctly; the collector is not told how to retain the association between data and specimens after the latter have been kept "all day" in a vasculum or lard can! A useful feature is a series of five outline maps showing the geographical coverage of the principal manuals and floras of the United States and North America; it is unfortunate, however, that references to three useful floras are omitted from maps I and II—Jepson, W. L. Manual of the flowering plants of California; Kearney, T. H., and R. H. Peebles, Arizona Flora; and Tidestrom, I. Flora of Utah and Nevada.

Judged strictly within its avowed limitations, this small volume should prove a useful teaching aid in both field and laboratory.—LINCOLN CONSTANCE.

## NOTES AND NEWS

INDEX TO PLANT CHROMOSOME NUMBERS. The need for up-to-date coverage of the literature dealing with plant chromosome numbers has led to an undertaking designed to compile and publish in annual installments a chromosome index for the entire plant kingdom.

This is being done by a group of botanists who are reviewing some two hundred journals and are listing all original chromosome counts occurring therein, except those resulting from endopolyploidy or deviating because of experimental treatment.

The Index, compiled from the journals of a single year, will be published annually within the shortest possible time after the last issue of each journal is available. In addition, there is planned a supplement containing counts published in previous years, but hitherto not indexed. Each issue of the Index will contain a complete bibliography for the counts included in that number.

The Index is published by the California Botanical Society. The first issue, supported by grants from the University Research Council of the University of North Carolina, and the National Science Foundation, went to press in May, 1958. It covers the 1956 journals, from which over 2000 listings have been taken. Produced by offset process on  $8\frac{1}{2} \times 11$ -inch paper, and punched for loose-leaf binders, it is priced at \$1.00. Orders (except from libraries and institutions) must be accompanied by payment and may be sent to C. Ritchie Bell, Department of Botany, University of North Carolina, Chapel Hill, North Carolina.

Further information can be obtained from Marion S. Cave, Research Associate, Department of Botany, University of California, Berkeley 4, California.

Some publications of interest follow:

*Drawings of British Plants*, by Stella Ross-Craig. Part X. Saxifragaceae–Crassulaceae. 33 pls. 1957. 8s. 6d. G. Bell and Sons, Ltd., London.

*Polemoniaceae of Nevada*, by Edgar T. Wherry; *Ipomopsis and Gilia Sect. Arachnion*, by Verne Grant and Alva Grant. Contributions toward a flora of Nevada, No. 43, pp. 1–103. Plant Industry Station, Beltsville, Maryland. Unbound, printed in offset.

*Systematic Anatomical Studies on Myrrhidendron and Other Woody Umbellales*, by Rafael Lucas Rodríguez. University of California Publications in Botany 29(2): 145–318, pls. 36–47, 69 figs. in text. 1957. \$3.50. University of California Press, Berkeley 4, California.

*The Structure and Reproduction of Some Members of the Rhodymeniaceae*, by Shirley Ray Sparling. University of California Publications in Botany 29(3): 319–396, pls. 48–59, 15 figs. in text. 1957. \$1.50.

*Guide List to Plants–Strybing Arboretum San Francisco*, by Eric Walther and Elizabeth McClintock. 1–76, 1958. Paper cover, \$1.00; cloth, \$3.00. Strybing Arboretum Society, San Francisco, California.

*Los Pastizales de Durango. Estudio Ecologico, Fisiografico y Floristico*, by Howard Scott Gentry. 1–361. 1957. 30 figs. in text. Instituto Mexicano de Recursos Naturales Renovables, A. C., Mexico, D. F. (Translated by Efraim Hernandez Xolocotzi.)

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Shorter items, such as range extensions and other biological notes, will be published in condensed form with a suitable title under the general heading, "Notes and News."

Institutional abbreviations in specimen citations should follow Lanjouw and Stafleu's list (*Index Herbariorum*. Part 1. The Herbaria of the World. Utrecht. Second Edition, 1954).

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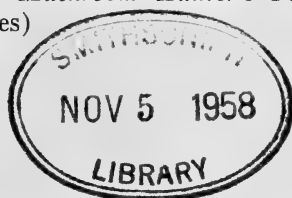
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## A WEST AMERICAN JOURNAL OF BOTANY

Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price \$4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

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OBSERVATIONS CONCERNING THE LIFE CYCLE OF  
SPONGOMORPHA COALITA (RUPRECHT) COLLINS

G. J. HOLLENBERG

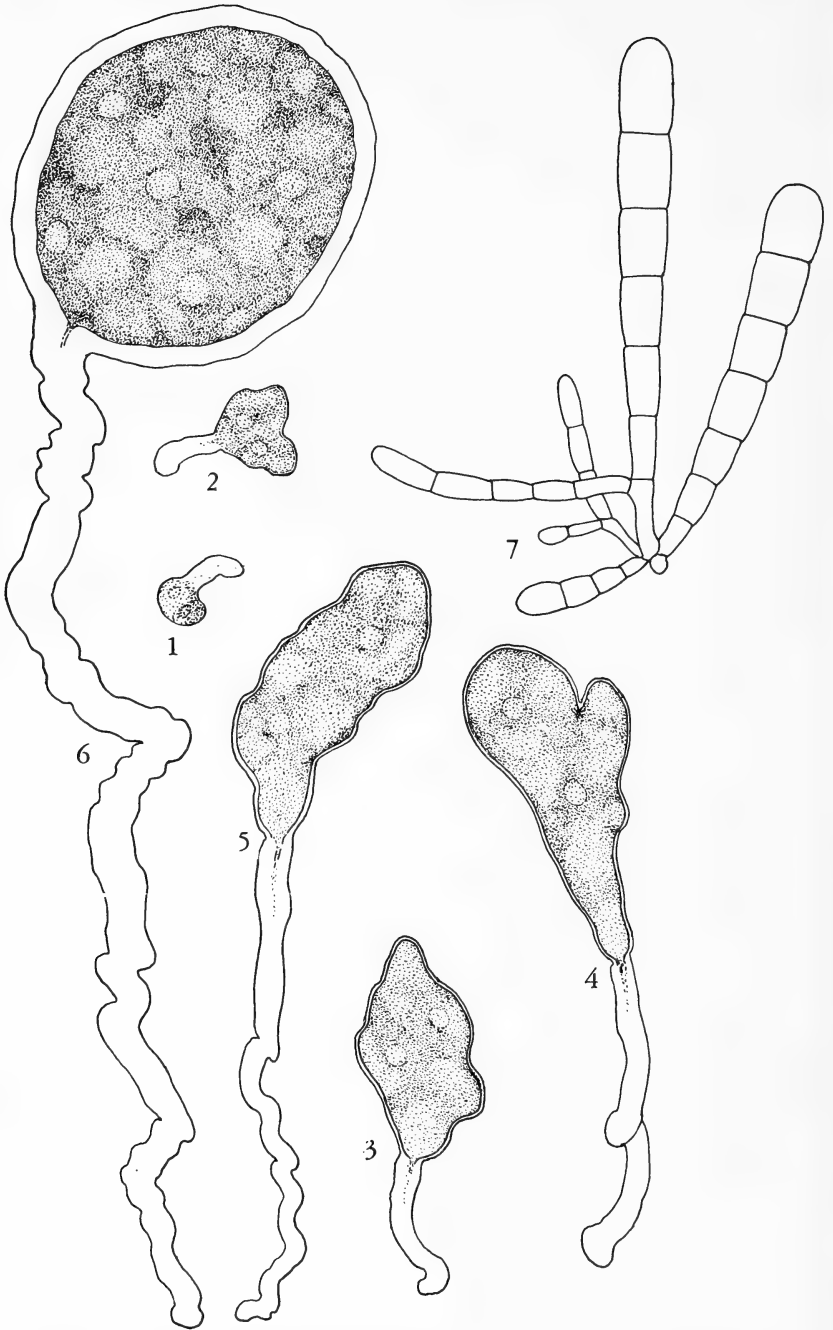
The work of Smith (1947) showed that in *Spongomorpha coalita* all plants are sexual, producing biflagellate gametes only. Smith concluded that this species of *Spongomorpha* does not exhibit an isomorphic alternation of generations. He observed that zygotes are negatively phototropic but did not follow their development.

During the summers of 1953–1956 inclusive the writer made culture studies of this plant at the Hopkins Marine Station at Pacific Grove, California. The cultures were kept in a cool humid basement room with northern light at 16–20° C. Discharge of gametes was obtained in a manner similar to that described by Smith. Advantage was taken of the negative phototactic response of the fusing gametes, also described by Smith, in getting cultures of zygotes relatively free of diatoms. The culture solution was sea water which had been heated nearly to the boiling point and allowed to cool. Nutrients were added as described for previous cultures by the writer (Hollenberg, 1939).

The zygotes are very small, measuring mostly 3–4  $\mu$ . in diameter. Smith states that the gametes lack a pyrenoid. The writer likewise observed no pyrenoid in the gametes, but very young germlings (figs. 1–3) showed two distinct pyrenoids. At this stage the chromatophore seemed to be of a reticulate nature. Perhaps more than one was present.

Within a few days it became evident that the original outgrowth of the zygote, which forms during germination, constituted a colorless rhizoidal outgrowth. Within two or three weeks it seemed apparent that this rhizoidal outgrowth represented some sort of attachment or penetration organ (figs. 3–6). Growth of the unicellular structure was very slow and no cross walls appeared, but as the rhizoidal process elongated the original cell became more or less spherical and gradually enlarged. When about 30 days old many of the germlings had become as much as 30  $\mu$ . in diameter, with thick walls and dense chromatophore with a number of pyrenoids (fig. 6). The rhizoidal process was up to 100  $\mu$ . long and mostly very contorted.

Although the pigmented cells increased slightly more in diameter, they seemed to become dormant and in most cases finally died or were overrun with diatoms. However, the culture started on July 19, 1955, remained alive until October 29, 1955, when it was discovered that several branching multicellular plants had developed from the unicellular germlings on the squares of cover glass in the culture dishes. The cells of these plants contained each a reticulate chloroplast and a number of pyrenoids. One of these plants had reached a length of 2 millimeters, but unfortunately the culture had become so overgrown with diatoms that the diminutive



FIGS. 1-6. Stages in the germination and growth of zygotes of *Spongomorpha coalita*,  $\times 1600$ .

FIG. 7. Multicellular plantlet developing from a *Spongomorpha* zygote,  $\times 35$ .



plants soon died. Since these multicellular plants developed directly from the bulbous part of the unicellular germlings on the pieces of coverglass, no free-swimming zoospores were involved in their development under the particular culture conditions.

In the cultures of the following summer no multicellular plants were obtained.

The slow growth and seeming dormancy of the zygotes and the development of the rhizoidal outgrowth, as well as the fact that the germlings continued to remain unicellular, suggested early in this study that they were probably some endophyte such as *Codiolum*. Several unsuccessful efforts were made to find *Codiolum* during the summer season in order to explore a possible relationship of this plant to *Codiolum*. Possibly *Codiolum* is seasonal in its appearance.

The failure to find zoospores arising from the unicellular germlings, and the failure of the multicellular plants arising in the cultures to develop to the stage in which the characteristic hooks arise on the branches, leaves some gaps in the suggested life cycle, but there seems to be little reason to doubt that the multicellular branched plants were young *Spongomorpha* plants. However, the culture studies on this plant have been discontinued because another investigator, Kung Chu Fan, is studying this problem. His more conclusive studies will be reported in the literature soon. Preliminary reports of Fan's work (1957) and that of the writer (Hollenberg, 1957) have been previously given.

It should also be noted that Jónsson (1957) has shown that a life cycle similar to the one suggested above for *Spongomorpha* occurs in the case of a closely related genus *Acrosiphonia*.

In summary, the above study shows that zygotes of *Spongomorpha coalita* developed slowly in the cultures into unicellular germlings with contorted rhizoidal outgrowths and that some of the germlings gave rise to branched multicellular plants believed to represent young *Spongomorpha* plants. The unicellular stage is believed to be an endophyte similar to or identical with *Codiolum*.

Department of Biology,  
University of Redlands,  
Redlands, California.

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## ABERRANT AMARANTHUS POPULATIONS OF THE SACRAMENTO-SAN JOAQUIN DELTA, CALIFORNIA

JOHN M. TUCKER AND JONATHAN D. SAUER

In the early 1890's W. L. Jepson found some tall, brightly colored amarantths growing among other rank vegetation on the riverbanks and small islands of the lower Sacramento River (Jepson, 1893, p. 243; 1914, p. 449; also Table 1). Although these were growing in natural habitats, he interpreted them as feral derivatives of an introduced cultigen which he identified as *Amaranthus hypochondriacus* L. We believe that Jepson was right in looking toward cultivated ornamental species for an ancestor of these striking plants, but their ancestry is different and more complex than he thought.

At present similar robust amarantths, on occasion attaining heights of as much as nine feet, often with gaudy anthocyanin pigmentation and great compound inflorescences, grow widely through the lowlands above the junction of the two major Central Valley rivers. They can still be found along the river side of levees but are now far more abundant as weeds in cultivated fields. It is apparent that they occur in very large part on the highly organic, peaty, basin soils—Staten peaty muck, Venice peaty muck, and Egbert muck—occupying the bulk of the delta country, as well as on more limited areas of alluvium—Burns clay loam, Ryde clay loam, Sacramento loam. They are abundant up to the edge of the peat soil and then peter out rapidly on the generally more alkaline alluvial loams along the periphery of the delta area.

### MORPHOLOGY

Field observation and examination of the few conventional herbarium specimens available from the area (Table 1) established that the delta amarantths are highly variable and include individuals that resemble various recognized species but rarely appear identical with any of them. In one population or another through this region characters of five different species are discernible, although in no population yet studied are the characters of all five present. These are all rather closely related members of the section *Amaranthotypus* Dumort. Descriptions and diagrammatic figures illustrating diagnostic features of these species are presented elsewhere (Sauer, 1950). It will suffice here to tabulate briefly the typical condition, or norm, of each species in four important structures (Table 2).

### POPULATION SAMPLES

In order to get beyond the frustration and uncertainty that come with attempts to understand taxonomically difficult populations from a few isolated specimens, mass collections were made at widely scattered localities through the delta (Table 1). Individuals were collected at random in sufficient numbers to give a respectable sample of the actual popula-

TABLE 1. ABERRANT AMARANTHUS COLLECTIONS FROM THE DELTA AREA

COLLECTOR AND NUMBER (DATE)	HERBARIUM (ACCESSION)	HABITAT AND LOCALITY	POSTULATED PARENTAGE
<i>Conventional Herbarium Specimens</i>			
W. L. Jepson (Oct. 4, 1893)	JEPS	Tyler Island, Sacramento County	<i>A. cruentus</i> x <i>A. retroflexus</i>
W. L. Jepson (Oct., 1895)	UC (7574)	Lower Sacramento	<i>A. cruentus</i> x <i>A. retroflexus</i>
R. N. Raynor (Aug. 11, 1941)	DAV (51)	Asparagus field, near Clarksburg, Yolo County	<i>A. caudatus</i> x <i>A. retroflexus</i>
C. O. Sauer and J. D. Sauer 1502 (Oct., 1947)	WIS	Roadside levee, Sherman Island, Sacramento County	<i>A. cruentus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>
J. D. Sauer 1643 (Aug. 14, 1953)	DAV, WIS	Farmyard ditch, Roberts Island, San Joaquin County	<i>A. caudatus</i> x <i>A. hybridus</i> x <i>A. powellii</i>
<i>Population Samples</i>			
J. M. Tucker 2314 (Oct. 31, 1951) 14 individuals	DAV, WIS	Periphery of cornfield, Staten Island, San Joaquin County	<i>A. caudatus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>
J. M. Tucker 2335 to 2343 (March 29, 1952)	DAV	Progeny of certain individuals from previous collection (2314) grown in greenhouse.	
J. M. Tucker 3277 (Oct. 27, 1956) 17 individuals	DAV	Milo field 1 mile west of Thornton, San Joaquin County	<i>A. cruentus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>
J. M. Tucker 3278 (Oct. 27, 1956) 47 individuals	DAV, WIS	Asparagus field 2½ miles west of Thornton, San Joaquin County	<i>A. cruentus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>
J. M. Tucker 3279 (Nov. 10, 1956) 16 individuals	DAV	Asparagus field, Roberts Island, San Joaquin County	<i>A. cruentus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>
J. M. Tucker 3280 (Nov. 10, 1956) 21 individuals	DAV, WIS	Open field, Union Island, San Joaquin County	<i>A. hybridus</i> x <i>A. powellii</i> x <i>A. retroflexus</i>

tion. In most cases only a few inches of the terminal portion of the inflorescence was collected and pressed. From some of these open-pollinated individuals progenies were grown in the greenhouse which, in cases where the number of individuals was small, were studied in their entirety, or, where the number of individuals was large, in random samples.

Each individual specimen was scored for its degree of resemblance to the five species in Table 2 in the characteristics tabulated. Discrimination between these taxa relies heavily on shape differences in the almost microscopic flower parts. It is practically impossible to abstract these effectively by simple measurements, but they can be scored by comparison with a graded series of specimens used as standards. These scorings have been rechecked and found to be repeatable with only minor variation.

TABLE 2. DIAGNOSTIC CHARACTERISTICS OF THE SPECIES INVOLVED IN THE DELTA AMARANTH COMPLEX

	TEPAL	BRACT	UTRICLE	INFLORESCENCE
<i>A. caudatus</i>	Long, very broadly obovate or spatulate, tip obtuse or emarginate, recurved.	Short or medium length, midrib very slender, rather long excurrent.	Style-branches recurved with slender bases forming shallow saddle.	Thick and pendulous, terminal spike extremely long, laterals few and short or absent.
<i>A. cruentus</i>	Extremely short, oblong, tip acute, straight.	Extremely short, midrib extremely slender, long excurrent.	Style-branches erect with slender bases forming sharp cleft at summit of very narrow tower.	Moderately thick, very lax, terminal spike short, laterals long, extremely numerous and crowded.
<i>A. hybridus</i>	Medium length, oblong, tip acute, straight.	Moderately long, midrib medium thick, long excurrent.	Style-branches erect with slender bases forming sharp cleft at summit of moderately narrow tower.	Moderately slender, lax, terminal spike short, laterals short, numerous, and crowded.
<i>A. powellii</i>	Very long, oblong, tip acute, straight.	Extremely long, midrib very thick, excurrent.	Style-branches recurved with stout bases forming cleft at summit of broad tower.	Thick and stiff, terminal spike long, laterals long, few and widely spaced.
<i>A. retroflexus</i>	Very long, narrowly obovate, tip emarginate, recurved.	Extremely long, midrib extremely thick, barely excurrent.	Style-branches erect with moderately stout bases forming saddle or shallow cleft.	Extremely thick and stiff, terminal spike short, laterals short, numerous, and crowded.

Data obtained in this way are presented in figures 1 to 3. Each small triangle represents an individual plant; its position relative to the apices of the grid indicates in a relative way resemblance to any of three species; the barbs on each symbol show scoring of separate diagnostic characters; shading inside the symbol indicates a peculiarity which is not taxonomically diagnostic. A detailed legend is given with figure 1. For example, in collection 2314 there are four plants shown in the lower left corner; all of these resemble *A. powellii* S. Wats. in all four characters studied, more than they resemble the other two species involved, but one plant slightly resembles *A. retroflexus* L. in all four characters and another slightly resembles *A. caudatus* L. in its bract structure. Toward the lower right corner of the same grid are two highly sterile plants which resemble *A. caudatus* more than *A. retroflexus* in tepal structure, but are closer to *A. retroflexus* in the other three characters.

In three of the population samples listed in Table 1 (Tucker 3277, 3278, and 3279) the same species were involved—*A. cruentus* L., *A. powellii*, and *A. retroflexus*. Since results of the analyses were quite similar in all three, only one (3278) is shown graphically (fig. 3).

It is evident from these graphs that the delta amaranth populations have variation patterns which are intelligible but extraordinarily complex. Instead of the monotonous repetition of character sets found in ordinary species sampling, these collections show reshuffling in a rich variety of individual combinations of several character sets. Characters of two species, *A. retroflexus* and *A. powellii*, recur in each field collection, while a third element alternates between characters of *A. hybridus* L., *A. cruentus*, and *A. caudatus*. Fortunately for the task of graphic representation, populations with more than three elements have not yet been encountered!

#### DISCUSSION

Recent hybridization between the five species mentioned seems the best explanation of the genesis of these populations. There is a loose but definite tendency for characters in the intermediate individuals to associate in the same combinations that are constant in the extremes—the recognized species. This is evidence of recent gene recombination hindered by old linkages that were established during more effective breeding discontinuity. This discontinuity may have resulted primarily from the former geographic segregation of the species, discussed below. If so, spatial isolation has been reinforced by secondary sterility barriers. High sterility is common in raw hybrids between *Amaranthus* species. For example, Murray (1940, p. 416), in many experimental interspecific crosses, obtained almost sterile  $F_1$ 's bearing only a few seeds to an entire inflorescence. Some of these crosses involved species in the delta complex—*A. caudatus*, *A. hybridus*, *A. powellii*, and *A. retroflexus*.<sup>1</sup>

Highly sterile plants, similar morphologically to certain of Murray's specimens, occur sporadically in the delta populations, but some apparent hybrids are not at all sterile. At first glance this recovery of fertility suggests amphidiploidy, but actually the hybrids must have regained fertility by some more subtle mechanism. Several progenies (from Tucker 2314, 3278, etc.) have been examined cytologically by Dr. Walter Plaut of the University of Wisconsin and Dr. W. F. Grant of McGill University and found to have the usual *Amaranthus* diploid number.

Another peculiarity which emerges in many individual delta amaranths is failure of the mature utricle to dehisce. Each of the field collections contains both dehiscent and indehiscent types; offspring of known "mother" plants usually but not always are like their mothers in this respect. Indehiscent utricles are an anomaly among all the species involved here. There are other sections of the genus in which indehiscence is the rule, but there is no trace of their other characteristics in these populations.

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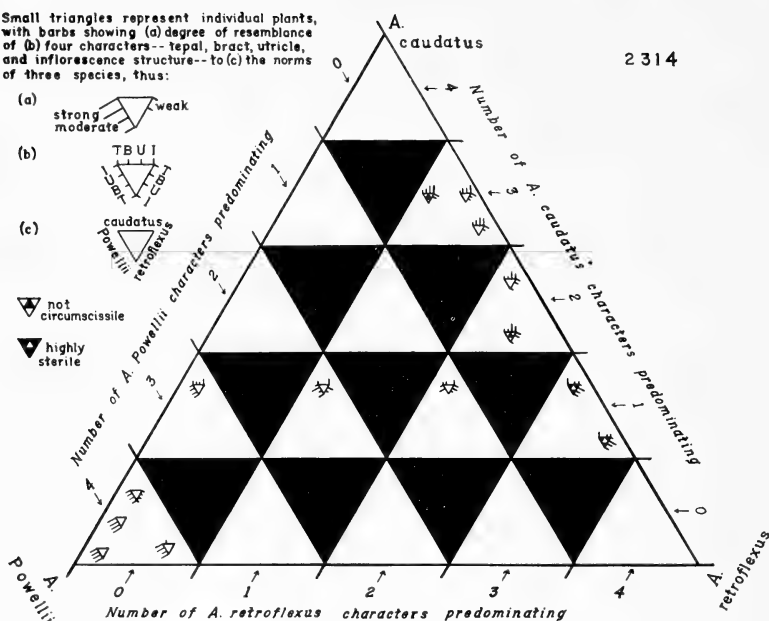
<sup>1</sup> In referring to this work it is necessary to revise a few of the original species determinations (Sauer, 1953).

Small triangles represent individual plants, with bars showing (a) degree of resemblance of (b) four characters--tepal, bract, utricle, and inflorescence structure--to (c) the norms of three species, thus:

- (a) strong moderate weak  
(b) TBU I  
(c) caudatus Powellii retroflexus

▲ not circumscissile

▲ highly sterile



Legend same as above.

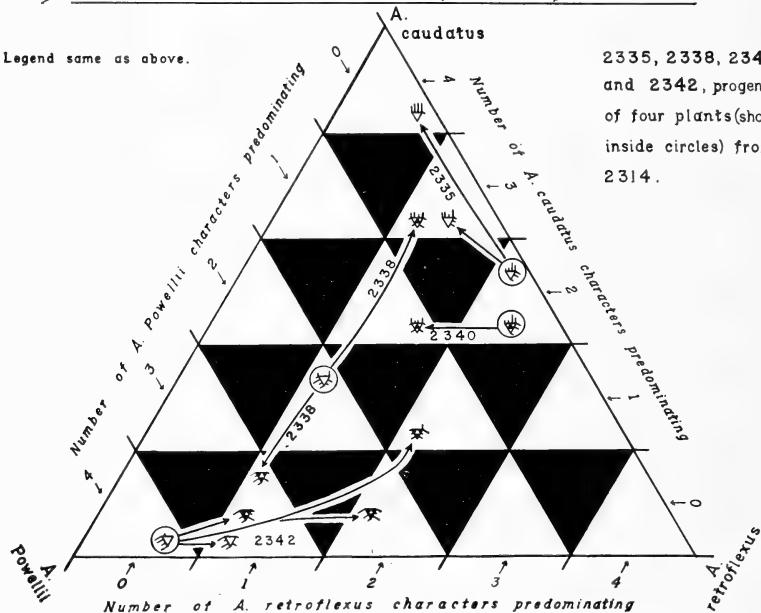


FIG. 1. Character combinations in a delta amaranth population sample, and in progenies of four of its members.

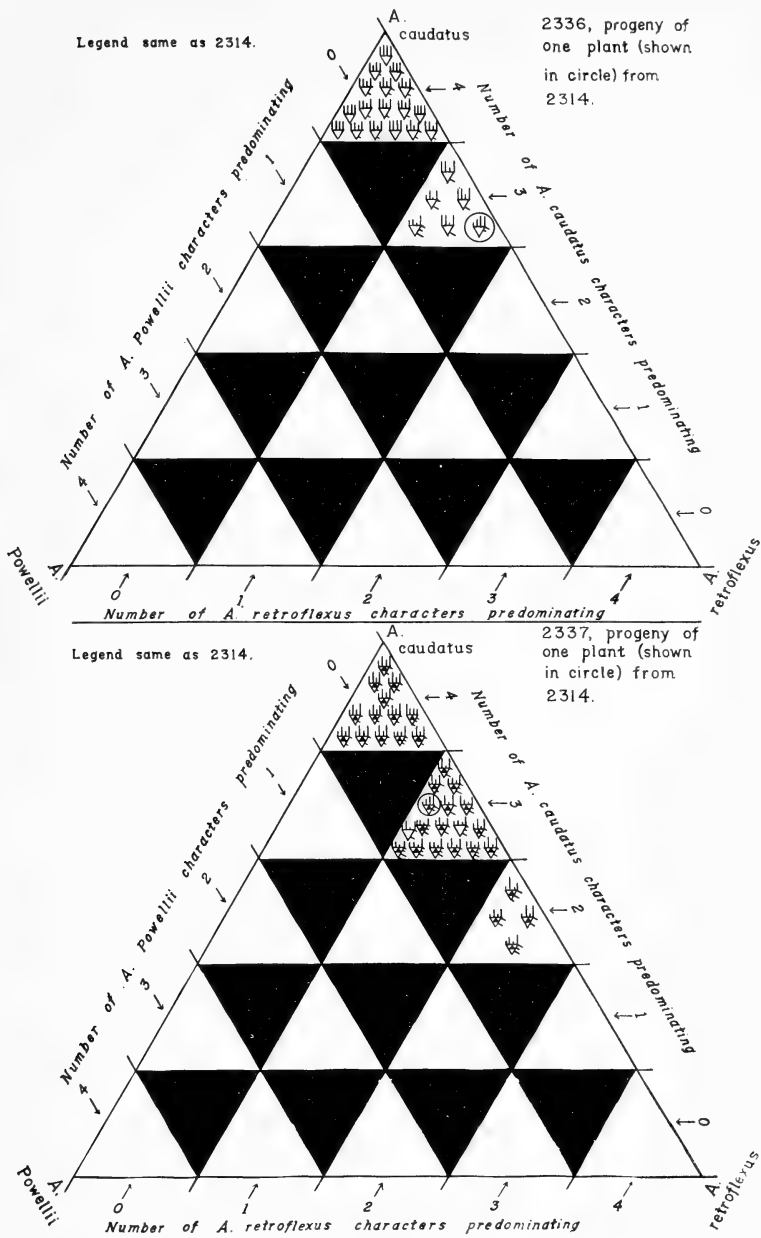


FIG. 2. Character combinations in progenies of delta amaranths.

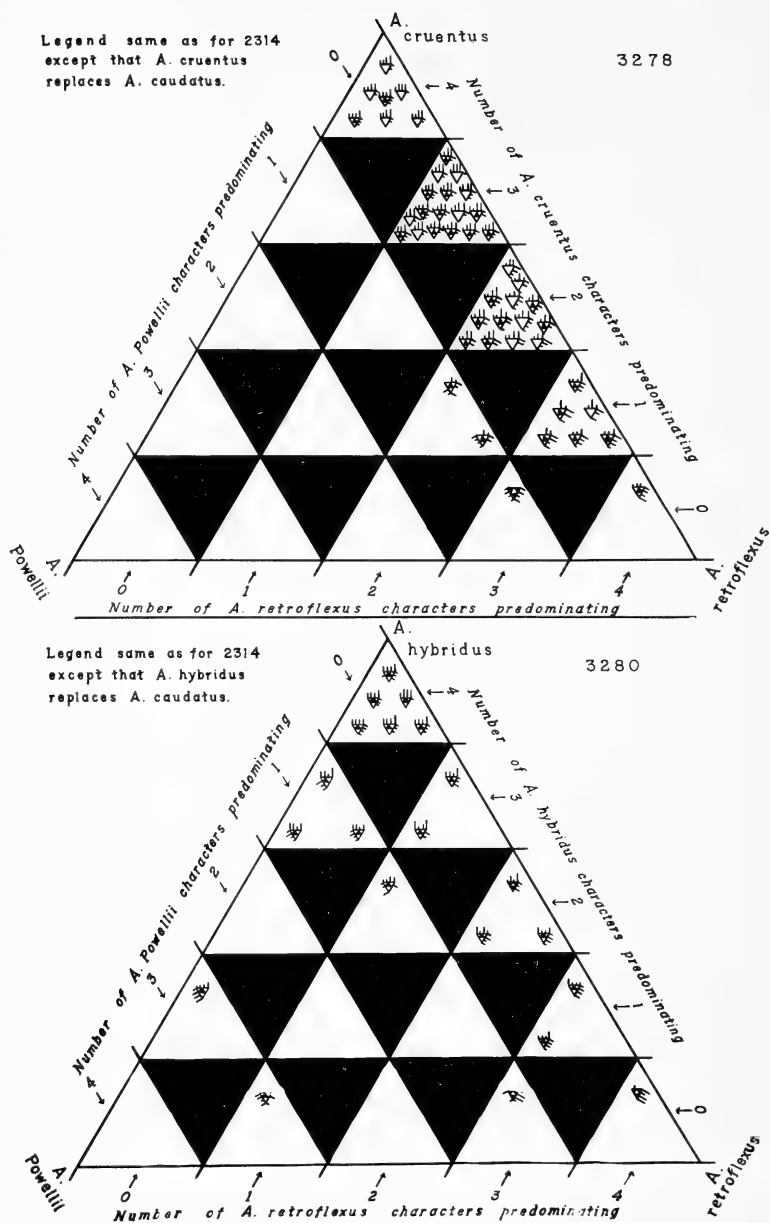


FIG. 3. Character combinations in delta amaranth population samples.



It seems likely that indehiscence in this group should not be regarded as a positive character traceable as a unit to distant ancestral species, but rather as simply a loss or breakdown of the mechanism controlling circumscission of the utricle in some hybrid genotypes. Thellung (1926) proposed the name *A. bouchoni* for similar plants which turned up as adventives in Europe, but he expressed uncertainty as to whether he was dealing with a new species or merely a form of ordinary *A. hybridus*. A heterogeneous lot of similar plants have been collected in many parts of the world. In the herbarium they mostly bear, perhaps properly, the name of some ordinary dehiscent species which they closely resemble.

Four of the five species which have joined forces in the delta area are natives of distant regions of America (Sauer, 1950). Only *A. powellii* appears to be native to the western United States. It is now mainly a weed of artificial habitats, but it is still found in what may have been its original habitat: naturally open sites along stream channels. It is conceivable that it was in the delta area in aboriginal times and has merely spread locally as the tule marshes were converted to modern farms.

The other species are probably late arrivals whose appearance in the delta country could hardly have antedated its opening to agricultural exploitation. The earliest attempt to reclaim any of this tule land for cultivation was evidently in the late 1850's (Hoag, 1872, p. 338), when a few farmers settled on Sherman Island, the southwestern extremity of present-day Sacramento County. The phenomenal productiveness of the fertile peat soil and California's Swampland Act of 1861 encouraged the reclamation of additional areas (Calif. Dept. Public Works, Div. Water Resources, 1931, p. 157). Results of early efforts were often temporary, however, and only about 15,000 acres had been reclaimed by 1870. During the next decade the area increased apace, and by 1880 a total of about 107,000 acres had been reclaimed. Reclamation continued at a fairly rapid pace to as late as 1920 (*op. cit.*, p. 158).

Other amaranth species have been found among the vegetable remains in old adobe bricks from the California mission period (Hendry and Bellue, 1925), and one of our species, *A. retroflexus*, was reported from 18th century bricks of Tumacacori Mission in Arizona (Hendry, 1931, p. 117). Other early reports of *A. retroflexus* and *A. hybridus* can be found in California botanical literature, but in the absence of contrary evidence from actual specimens such records may show nothing but taxonomic confusion. Early botanists were slow to recognize the western *A. powellii* as distinct from superficially similar eastern species, and in older herbarium determinations *A. powellii* usually masquerades as *A. retroflexus* or *A. hybridus*. In the 1890's *A. retroflexus*, *A. cruentus*, and *A. caudatus* begin to join *A. powellii* in the herbarium record from California; *A. hybridus* appears after 1900.

The backgrounds of these immigrants are diverse. *Amaranthus hybridus* probably originated in tropical America; it is now the commonest weed amaranth there and in the southeastern United States. Contrary to

oft-repeated statements in taxonomic manuals, *A. retroflexus* is unknown in the tropics; it is a conspicuously successful weed in eastern Canada and the eastern United States, where it probably originated. Although centered much farther north, its range widely overlaps that of *A. hybridus*. *Amaranthus cruentus* and *A. caudatus* are cultigens, developed as grain crops by ancient Indian peoples of Central America and the Andes, respectively. *Amaranthus cruentus* was apparently derived from *A. hybridus*, *A. caudatus* from *A. quitensis* H.B.K., a species not known to be present in California. Both of these old Indian crop species have been widely distributed as ornamentals, often by commercial seed houses.

The introduction of these weedy and ornamental amaranths into California is in no way remarkable—all of them have immigrated into many parts of the world in modern times. Nor is the mere fact of hybridization between these species especially noteworthy. Two things do, however, impress us as being quite remarkable: firstly, the fact that the introduced ornamentals have not begotten just a few ephemeral escapes and abortive hybrids as is the rule elsewhere, but rather have made a spectacular contribution to successful weed populations. Secondly, despite their evident success in the delta country, these ornamentals and their hybrids have not spread beyond the area, but seem to be rather closely confined to it.

The two facts are in all probability closely interrelated. As with so many of man's vegetable creations, in the case of the two cultigens, *A. caudatus* and *A. cruentus*, selection has most likely been for rapid growth, large size, and high yield, *given* cultivation, *given* fertile soil, and *given* a moisture supply through the growing season. Whatever drought resistance their ancestors may have had, whatever ability to flourish under adverse soil conditions—most of this may well have been lost long since. As with the cultigen species, so with their hybrids in the delta region. Given a light and highly fertile organic soil,<sup>2</sup> a constant moisture supply, due to a high water table, and a long, warm growing season, these hybrids, by virtue of their more robust stature and often prodigious fecundity, can out-compete—as field weeds—their ruderal parents, *A. hybridus*, *A. powellii*, and *A. retroflexus*. However, the very circumstance of their ornamental parents' having evolved as cultigens is the undoing of the hybrids under conditions much less than optimal, keeping them from successfully invading areas that lack the highly organic soil, abundant moisture, and other favorable conditions which prevail in the delta.

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<sup>2</sup> After four years of experimental work on improving asparagus yields, G. C. Hanna (1939) had found no fertilizer which would improve yields on Ryer Island soils!

Department of Botany,  
University of California, Davis  
and

Department of Botany,  
University of Wisconsin, Madison

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THE GENUS *ERYSIMUM* (CRUCIFERAE) IN NORTH AMERICA NORTH OF MEXICO—A KEY TO THE SPECIES AND VARIETIES

GEORGE B. ROSSBACH

This key to twenty-three species and eight varieties of *Erysimum* is a result of detailed analysis of the specimens in various American herbaria plus collections of the writer from areas throughout most of the range of these taxa in the United States. Many morphological interrelationships exist among the various taxa, these usually manifesting themselves as local geographical forms which presumably have a genetical-ecological basis. Some of these forms are of sufficient magnitude to be treated as varietal entities. In a careful attempt to express much of this variability in the key, it frequently has been necessary to rely for identification upon a combination of many characteristics, to refer to exceptions and make cross-references, and to key three taxa twice. However, with understanding of the diagnostic characteristics and realization of the close relationships, the great majority of plants can be relegated to reasonably definite taxa. In order to present a survey of geographical distribution, a summary of the range of each taxon is added to the key.

Although the genus is native south through Mexico into Guatemala, taxa presumably limited to these countries are omitted due to insufficient representation. Thus at least two probably acceptable Mexican species,

*Erysimum Tilimi* J. Gay and *E. macradenium* J. Gay, are excluded from this key. Forms of *E. capitatum* (Dougl.) Greene, *E. insulare* Greene, and possible forms of *E. argillosum* (Greene) Rydb. also occur in Mexico as well as northward.

- A. Petals small, 3–13 mm. long, just under 1–5 mm. broad; seeds 2 mm. long or much shorter, 1 mm. broad or narrower.
- B. Annuals.
- C. Axis of mature raceme geniculate; siliques divaricate, (4–)6–8(–8.5) cm. long, moniliform at maturity; pedicels consistently short, under  $\frac{1}{3}$  as long as siliques, nearly as thick as siliques, 1–1.5 mm. thick; margins of leaves repand-dentate. Widespread weed from Europe.....*E. repandum* L.
- CC. Axis of mature raceme straight; siliques more or less ascending, very short, (1–)1.5–2(–3.5) cm. long, not moniliform, plump; pedicels of various lengths,  $\frac{1}{3}$  to  $\frac{1}{2}$  as long as siliques, much more slender than siliques, not over and usually under 0.6 mm. thick; margins of leaves sparingly denticulate, often some entire. Widespread, often as a weed, native and from Europe.....*E. cheiranthoides* L.
- BB. Biennials or short-lived perennials, the latter usually at high altitudes, far north or coastal.
- D. Siliques 2–3 cm. long as known in North America, in Europe also to about 10 cm.; cauline leaves sparingly and shallowly denticulate on our plants. Weed from Europe, known in Ontario and Quebec.....*E. hieracifolium* L.
- DD. Siliques 4–10 cm. long, rarely less; cauline leaves usually entire.
- E. Petals 1–3 mm. broad; lower leaves often broadly and usually bluntly oblanceolate, broadest very near apex, not callose.
- F. Leaves usually cinereous, sometimes not so in cooler environments, as locally in northwest portion of range, usually not crowded; stems almost always single, or if more than one, usually strict; petals usually pale yellow, usually under 10 mm. long, usually 2 mm. or less broad. Great Lakes (local), to Nevada and Alaska.....*E. inconspicuum* (S. Wats.) MacMill.
- FF. Leaves not at all or scarcely cinereous, usually crowded; stems often more than one, spreading-ascending; petals usually rich yellow, usually 10 mm. or more long, 2 mm. or more broad. Local on Gulf of St. Lawrence and Newfoundland.....*E. inconspicuum* var. *coarctatum* (Fern.) G. B. Rossbach<sup>1</sup>
- EE. Petals 3–5 mm. broad, as known; lower leaves narrowly elongate, linear-oblanceolate, acute or subacute, callose. Known locally from desert of southern New Mexico . . . *E. desertorum* (Woot. & Standl.) G. B. Rossbach
- AA. Petals larger, 13–32 mm. long, rarely as short as 7 mm. (P–PP), (3–)+3–15 mm. broad; seeds larger, usually 2 mm. or more long, usually 1 mm. or more broad (except J).
- G. Leaves never approaching a filiform shape, some or all as much as 2 or more mm. broad.
- H. Plants not suffrutescent, the caudex not notably elongate or long-branched above ground, erect, or at least not sprawling or widely spreading, sterile branches absent, or if present, very short, not elongate; lowest leaves dropping, breaking or long-lived, but scarcely marcescent. A few plants tending toward characters of HH.
- I. Seeds wingless or bearing a small scarious distal appendage, very slightly to convexly compressed, variously shaped; siliques equally tetragonal to

<sup>1</sup> The taxa attributed to the author were published as follows: Rossbach, George B. 1958. New taxa and new combinations in the genus *Erysimum* in North America. *El Aliso* 4:115–124.

strongly compressed, equally to very unequally keeled. Not occurring on coast.

- J. Siliques very rigidly divaricate, equally or subequally tetragonal, with subequal, very protrusive keels prominent as four dark, less pubescent stripes; seeds small, about 1.5 mm. long, scarcely compressed, rather angular, almost always wingless; leaves narrowly oblanceolate, some or all dentate; foliar hairs crowded, quite strigose, 2-parted; stems rather low, commonly under 30 cm. to base of raceme. Great Plains, Black Hills, local prairie extensions into Rocky Mountains.....*E. asperum* (Nutt.) DC.
- JJ. Siliques ascending, occasionally becoming arching-divaricate when long and heavy, usually compressed, but ranging from subequally tetragonal to strongly compressed, very unequally to subequally keeled, not notably striped; seeds of variable size, more or less compressed, winged or wingless; leaves and stems variable.
- K. Leaves narrow, acute or subacute, usually thick, revolute and cinereous; foliar hairs 2-parted, usually crowded; siliques narrow, commonly about 1.5 mm. broad, subequally tetragonal to slightly compressed, most often subequally keeled, hairs usually crowded; seeds wingless or less often minutely winged, commonly not over 2 mm. long; petals yellow; stems usually low, commonly 8–30 cm. to base of raceme. Dry regions, mid-altitudes, mainly Rocky Mountains, Great Basin to eastern California, southwestern plateaus.....*E. argillosum* (Greene) Rydb.
- KK. Combination of characters not as above; foliar hairs 2- or 3-parted; siliques compressed, unequally keeled; otherwise variable.
- L. Some or all upper foliar hairs 3- or more parted, 2-parted hairs frequently also present, or locally in Southwest the hairs exclusively 2-parted; leaves usually dentate or denticulate, subacute to acute; siliques fairly protrusively keeled on flatter surfaces; seeds distally winged; fresh petals usually orange, also shades of yellow, brick-red, orange-brown, or locally in Southwest a purplish maroon, drying toward purple; stems usually tall, commonly 20–70(–135) cm. to base of raceme. Widespread, largely inland in hills, mainly Pacific states and east into Idaho, through southwestern states and locally east to Texas and northeast to Ohio; Mexico and southern British Columbia.....*E. capitatum* (Dougl.) Greene
- LL. Combination of characters not as above; foliar hairs usually but not always 2-parted; leaves variable; siliques with very slender, scarcely or non-protrusive keels on flattened surfaces; seeds variable; petals yellow, or some orange-yellow, or rose-red-purple (UU and TT); stems variable.
- M. Stems, except for impoverished individuals, robust and much-branched above, diameter near base commonly 4–12 mm., usually tall, about 12–60 cm. to base of raceme; foliar hairs usually dominantly 2-parted; seeds long, 2–4 mm., noticeably winged at distal end.
- N. Leaves elongate, linear-lanceolate, tapering gradually to quite acute apex, dentate, green; siliques slender, (1.5–)2(–2) mm. broad, seeds remote; caudex somewhat prolonged; stems tall, commonly 30–60 cm. to base of major raceme, usually near 5 mm. in diameter at base. Dunes by San Joaquin River east of Antioch, California.....*E. capitatum* var. *angustatum* (Greene) G. B. Rossbach

- NN. Leaves oblanceolate, rather blunt, entire or very sparingly and minutely denticulate, cinereous; siliques broad, 2-2.5 (-3) mm. across; seeds proximate; caudex not prolonged; stems usually shorter, over 5 mm. in diameter at base except for impoverished individuals. Mojave Desert and locally on edge of Carrizo Plain, California.....  
 .....*E. capitatum* var. *Bealianum* (Jepson) G. B. Rossbach
- MM. Stems slender, simple or occasionally sparsely or much (Q) branched, diameter near base under 4 mm., usually much less, usually low, about 0.5-22 (-50: O, S) cm. to base of raceme; otherwise variable.
- O. Plants not dwarf, stems slender, tall, 30-50 cm. to base of raceme, green or dull purplish green, usually bearing very small abortive axillary branches; leaves narrowly elongate, acute, (4-)6-9(-18) cm. long, (1-)2-5(-9) mm. broad; siliques long, slender, compressed, often purplish green, (6-)8-10(-13) cm. long, about 1.3-1.8 mm. broad; fresh petals orange to orange-yellow. See also E'E'. Sandy mesas near Lompoc, Nipomo, and Guadalupe, California .....  
 .....*E. suffrutescens* var. *lompocense* G. B. Rossbach
- OO. Plants dwarf, stems almost always under 20 cm. to base of raceme (some exceptions, S); otherwise variable.
- P. Leaves runcinate-dentate, linear-lanceolate to narrowly oblanceolate; foliar hairs 2-3-parted; petals always yellow.
- Q. Stems often several, major ones or all divaricately and rigidly long-branched; leaves cinereous, callose, basal ones drying by flowering time; siliques not purplish colored, not notably moniliform, not torulose. Deposits about hot springs south of Reno, Nevada.....  
 .....*E. capitatum* var. *washoense* G. B. Rossbach
- QQ. Stems single or less often several, almost always simple, the branches, if any, few, ascending, short, not rigid; leaves green, not callose, basal ones living through flowering time; siliques purplish colored, moniliform, often slightly torulose. Upper Mount Rainier, less typically on several other mountains of northwestern Washington.....  
 .....*E. torulosum* Piper
- PP. Leaves entire, not of one general shape, if dentate, usually broadly oblanceolate, or if linear and dentate, the petals usually rose-red-purple; foliar hairs usually 2-parted; petals yellow or purple.
- R. Leaves broadest very near apex, spatulate to oblanceolate, apex rounded, blunt or broadly angular; foliar hairs variable; sterile leaf rosettes present or absent.
- S. Siliques not torulose, scarcely or not moniliform, commonly 2-3 mm. broad, tapering gradually to varying degrees; style variably long, more or less slender, about 0.5 mm. thick; lower leaves spatulate to bluntly oblanceolate, not acute, entire or less often very sparingly denticulate or dentate; foliar hairs usually or dominantly 2-parted; caudex simple or shortly branched, rarely bearing sterile leaf rosettes; stems variable in height, (0.5-)2-30(-50) cm. to base of raceme. High mountains, Sierra Nevada and very locally north and east.....  
 .....*E. perenne* (S. Wats. in Coville) Abrams

- SS. Siliques torulose, curved in several planes, moniliform, not over 2 mm. broad, tapering very gradually and slenderly; style long, very slender, almost always under 0.5 mm. thick; lower leaves very shortly and broadly oblanceolate, not rounded, dentate; foliar hairs 2- often dominantly 3-parted; caudex multicapitous, becoming elongate if buried, bearing some sterile leaf rosettes; stems always low, 4-13 cm. to base of raceme. Known in alpine zone on Mount Steele and Mount Constance, Olympic Mountains, Washington....*E. arenicola* S. Wats.
- RR. Leaves not broadest very near apex, linear-lanceolate to oblanceolate, acute; foliar hairs 2-parted; sterile leaf rosettes often present.
- T. Petals yellow or rose-red-purple; raceme leafless and bractless.
- U. Foliar hairs crowded, strigose; very crowded leaves eventually marcescent on lower portions of stems, entire or very nearly so; petals yellow; seeds very elongate, 2-2.3 mm. long, 0.7 mm. broad. Known from vicinity of Dawson, Yukon.....*E. angustatum* Rydb.
- UU. Foliar hairs almost always sparse and delicate; leaves not marcescent, entire or few times dentate or denticulate; petals rose-red-purple or yellow; seeds obovate, 1.5-2 mm. long, 1-1.6 mm. broad. High altitudes in Rocky Mountains, most frequent in Colorado.....*E. nivale* (Greene) Rydb.
- TT. Petals always rose-red-purple; few to many of the lower pedicels subtended by or bearing bracts or leaves.
- V. Stems very low, (-1-)1-3(-5) cm. to base of raceme; leaves entire or very sparingly and shallowly dentate; only lowest few pedicels subtended by bracts. Widespread in arctic North America and Asia.....*E. Pallasii* (Pursh) Fern.
- VV. Stems taller, (8-)15-16(-18) cm. to base of raceme; lower leaves numerous and deeply dentate; many pedicels subtended by or some bearing a bract or small leaf. Known from Teller, western coast of Alaska.....*E. Pallasii* var. *bracteosum* G. B. Rossbach
- II. Seeds extensively winged about distal end and more or less along one side, strongly compressed, oval; siliques, at least when dry, very strongly compressed, unequally keeled.
- W. Style long, (2-)3(-5) mm.; leaves entire or occasionally sparingly denticulate, linear-oblanceolate, cinereous. Sands along middle Columbia River and nearby on tributaries....*E. occidentale* (S. Wats.) Robins.
- WW. Style shorter, scarcely present to 1(-2) mm. long; leaves variable, but not cinereous except in a northern form (Y). Coastal or near coast, or in case of *E. Cheiri* raised in gardens.
- X. Siliques stiffly divaricate, upcurved except for a few colonies not on dunes (under or near YY); pedicels divaricate.
- Y. Leaves oblong-spatulate or at least blunt, broadest toward base of stem, where measuring 4-13 (rarely -30) mm. broad; stems low, (1-)3-7(-13) cm. to base of raceme. Local on coastal dunes on and near Point Pinos, and Fort Bragg to several miles north, and on west side Humboldt Bay, California.....*E. Menziesii* (Hook.) Wettst.

- YY. Leaves linear-oblongate to oblongate, acute, becoming narrowly elongate toward base of stem, 1.5–3 (rarely –6) mm. broad; stems almost always taller, (3–)15–50(–83) cm. to base of raceme. Coastal sands along Monterey Bay; atypical forms along San Diego County and Santa Rosa Island, California.....  
.....*E. ammophilum* Heller
- XX. Siliques stiffly ascending, straight to slightly upcurved (though sometimes becoming arching-divaricate when long and lax); pedicels variable.
- Z. Stigma not bicornate, merely bilobed; leaves not soon deciduous, almost always regularly sinuate-dentate; foliar hairs usually dominantly 3-parted; petals rich yellow, yellow, or creamy white.
- A'. Leaves shortly oblongate, abruptly contracted to apex; siliques distally blunt or at least tapering abruptly to style; plants fleshy. Restricted to coastline, on bluffs and headlands, atypically and rarely on nearby dunes, locally from Point Reyes, Marin County, California, to The Heads, Curry County, Oregon.....  
.....*E. concinnum* Eastw.
- A'A'. Leaves linear-oblongate, elongate, almost always tapering rather gradually at both ends; siliques usually tapering gradually to style; plants not fleshy, sometimes very locally the coastal plants slightly so. See D' for unusual forms. Serpentine or sandy soil, near and only very locally on the coast, San Mateo County, and vicinity Mount Tamalpais, and at least formerly at Bodega Bay, California, and near mouth of Rogue River, Curry County, Oregon.....*E. franciscanum* G. B. Rossbach
- ZZ. Stigma bicornate, i.e. deeply divided, with long arching lobes; leaves always soon and progressively deciduous along the aging stout stem, entire or very sparingly and sharply serrulate-denticulate; foliar hairs 2-parted; petals variable in color, yellow, orange, brown-orange or with purplish hue. See also C'. Introduced from Europe, rarely persistent or escaped from gardens.....  
.....*E. Cheiri* (L.) Crantz
- HH. Plants suffrutescent, the caudex elongate, long-branched above ground, sprawling or widely spreading, bearing elongate sterile branches; leaves (except under C') becoming marcescent below. (A few plants tend toward characters of H.)
- B'. Seeds strongly compressed, extensively winged more or less along one side as well as about distal end; siliques compressed.
- C'. Stigma bicornate, i.e. deeply divided, with long arching lobes; leaves always soon and progressively deciduous along aging stem, entire or very sparingly and sharply serrulate-denticulate; foliar hairs 2-parted; petals variable in color, yellow, orange, brown-orange, or with purplish hue. See also ZZ. Not coastal in the Americas, introduced from Europe, rarely persistent or escaped from gardens.....  
.....*E. Cheiri* (L.) Crantz
- C'C'. Stigma not bicornate, only slightly 2-lobed; leaves not usually deciduous below, but more or less marcescent, almost always regularly sinuate-dentate; foliar hairs (2–)3(–many)-parted; petals rich yellow, yellow, or occasionally creamy white. Coastal or near-coastal.
- D'. Plants not fleshy, sometimes very locally the coastal plants slightly so; these unusual forms moderately suffrutescent and the sterile branches, if present, usually short; siliques usually tapering gradually to style, not fleshy, strongly compressed; style 1–2 mm. long; seeds not usually crowded; petals colored as above. See A'A' for



usual forms. Serpentine or sandy soil, near and only very locally on the coast, San Mateo County and vicinity Mount Tamalpais, and at least formerly at Bodega Bay, California, and near mouth of Rogue River, Curry County, Oregon.....*E. franciscanum* G. B. Rossbach

D'D'. Plants succulent; becoming suffrutescent, usually sprawling and branched and bearing some sterile stems; siliques tapering abruptly to style, fleshy, plump, but strongly compressed when dry; style -1(-1.8) mm. long; seeds usually crowded, often irregular in shape; petals rich egg-yellow. Coastal bluffs and headlands locally along San Mateo County and on near-coastal sandy slope in Santa Cruz County, California.....*E. franciscanum* var. *crassifolium* G. B. Rossbach

B'B'. Seeds not strongly compressed, convex, distally winged or wingless; siliques variable.

E'. Plants succulent, notably suffrutescent and sprawling-ascending, or sometimes spreading-upcurved (F'), much-branched, bearing long vegetative stems; leaves notably marcescent below; siliques coarse, squarish in cross-section or compressed variously, either at right angles to or parallel to septum.

F'. Plants suffrutescent, branched, usually spreading-upcurved; leaves narrowly linear-oblongate, (1.5-)2-3(-5-rarely 6) mm. broad; siliques compressed parallel to septum or squarish in cross-section. Coastal sands, southern Santa Monica Bay, and from Santa Maria River to southern Morro Bay, California.....  
.....*E. suffrutescens* (Abrams) G. B. Rossbach

F'F'. Plants strongly suffrutescent, much-branched, sprawling at base; leaves variable; siliques plump, abruptly contracted at both ends, replete with crowded, irregular seeds, squarish in cross-section to compressed at right angles to septum.

G'. Leaves comparatively broad, 3-12(-20) mm. broad, tending toward two types, one large and abruptly tapering to blunt apex, not recurved, often terminating sterile branches, the other narrower, more gradually tapering, recurved, occurring at any location, usually fleshier; foliar hairs sparse, (2-)3(-4)-parted. Coastal dunes between Arguello and Purisima points, and rocky maritime bluffs of Morro Rock near Morro Bay, California.....  
.....*E. suffrutescens* var. *grandifolium* G. B. Rossbach

G'G'. Leaves all narrow, 1.5-3(-5) mm. broad, essentially of one type; foliar hairs crowded, 2-parted. San Miguel and Santa Rosa islands of the North Channel Islands, California, and a form with somewhat blunt, smaller leaves on Guadalupe Island, Baja California  
.....*E. insulare* Greene

E'E'. Plants not at all fleshy, only moderately suffrutescent, not sprawling, only once or few-times branched, bearing few and rather short sterile stems; leaves only moderately marcescent below; siliques slender, always quite compressed parallel to septum. See also O. Sandy mesas near Lompoc, Nipomo, and Guadalupe, California.....  
.....*E. suffrutescens* var. *lompocense* G. B. Rossbach

GG. Leaves nearly filiform, 0.3-1.7 mm. broad; stems suffused with somewhat metallic purplish hue, normally simple; caudex more or less elongate, herbaceous to subligneous, single or divided. Miocene Santa Margarita sand deposit in Santa Cruz Mountains, California.....*E. teretifolium* Eastw.

West Virginia Wesleyan College,  
Buckhannon, West Virginia

## DR. JOHN McLOUGHLIN AND THE BOTANY OF THE PACIFIC NORTHWEST

ERWIN F. LANGE

Among the unrecognized contributors to the development of the botany of the Pacific Northwest is Dr. John McLoughlin, Chief Factor for the Hudson's Bay Company from 1824 to 1846 with headquarters at Fort Vancouver, situated on the northern bank of the Columbia River, 120 miles inland from the Pacific Ocean. From Fort Vancouver, McLoughlin ruled with dictatorial authority an empire that extended from California to Alaska and from the Rocky Mountains to the Pacific Ocean and which was inhabited only by savage Indians and white fur traders. Also at Fort Vancouver he was awarded the first medal for botany to be presented in the Pacific Northwest.

During these years the region was a virgin wilderness with the forts of the fur traders providing the only haven to which a weary traveller might turn for some degree of civilized comfort. The botany of the area was unexplored and challenged scientists of both America and Europe. Without the cooperation of the officials of the Fur Company the collecting of the new and interesting plants of the Northwest would have been delayed for many years. Of particular interest to the scientific history of the Pacific Northwest is the fact that all of the early botanical explorers were welcomed by Dr. McLoughlin so that during his years as Chief Factor, Fort Vancouver became in effect the scientific headquarters of what was then known as the Oregon Country.

In April, 1825, the first two scientists to explore extensively in the Pacific Northwest arrived from England just as McLoughlin was moving his headquarters from Fort George, Astoria, to Vancouver. These were Dr. John Scouler, naturalist, and ship surgeon on the Hudson's Bay Company's *William and Anne*, and David Douglas, botanist sent by the Horticultural Society of London.

Dr. Scouler remained in the Northwest but a few months collecting zoological and botanical specimens, and on his return to England he was the first scientist to describe in British scientific journals the practice of the Chinook Indians of flattening the skull of infants of the Indian aristocracy. Scouler met McLoughlin at Fort George and wrote of him in his diary:

From him I experienced the utmost politeness and to his kindness was indebted for some curious specimens of the rocks of the Rocky Mountains.

David Douglas, one of the most prolific botanical collectors of the Pacific Northwest, explored much of the Oregon Country during the years 1825-1827 and 1832-1833. His explorations were interrupted by a return journey to England.

On first meeting McLoughlin he noted in his diary:



FIG. 1. Dr. John McLoughlin. Portrait made about 1845. Courtesy of the Oregon Historical Society.

... I embarked in a small boat with Mr. John McLoughlin, the Chief Factor, who received me with demonstrations of the most kindly feelings, and showed me every civility which it was in his power to bestow.

Douglas showed McLoughlin his written instructions from the Horticultural Society and discussed his plans verbally. As a result of the conversation, Douglas wrote:

In the most frank and handsome manner he assured me that everything in his power would be done to promote the views of the society.

Fort Vancouver became the headquarters for Douglas as he radiated out in all directions to collect seeds, pressed specimens and living plants of an unknown and exciting flora. The Fort was used to dry and prepare his specimens, and pack them for shipment to England on board the ships of the Hudson's Bay Company. Dr. McLoughlin made all facilities of the Fort available to him including boats and horses for transportation.



FIG. 2. Fort Vancouver, 1845. Courtesy of the Oregon Historical Society.

For cooperating in promoting the study of botany in the Pacific Northwest, Dr. McLoughlin was awarded a silver medal by the Horticultural Society of London on May 11, 1826. This medal was the first scientific award made in the Oregon Country and is today on exhibit in the McLoughlin house, a public shrine, in Oregon City, Oregon. The *Transactions of the Horticultural Society* refer to the awarding of the medal as follows:

To John McLoughlan [sic], the Chief Factor of the Hudson's Bay Company, at the mouth of the River Columbia, for his assistance rendered Mr. David Douglas, whilst making his collections in the countries belonging to the Hudson's Bay Company in the Western part of North America.

After taking his final leave from the Oregon Country Douglas, whose name is today popularly associated with the Northwest's most important lumbering tree, the so-called Douglas fir, summarized the status of science in this wild country:

Science has few friends among those who visit the coast of North-West America, solely with a view to gain. Still with such a person as Mr. McLoughlin on the Columbia, they may do a great deal of service to Natural History.

The first two scientists to travel across the American continent reached Fort Vancouver in September, 1834. They were Thomas Nuttall, botanist and naturalist, who resigned his position at Harvard University in order to accompany Nathaniel Wyeth on his second overland expedition, and J. Kirk Townsend, a young Philadelphia ornithologist. Although Nuttall and Townsend had accompanied Wyeth who was attempting the establishment of a rival fur company under American auspices, they were well received by Dr. McLoughlin at Fort Vancouver.

Townsend recorded the events of the expedition in a delightful narrative in which he frequently referred to the activities of Dr. McLoughlin. Although he did not record any particular act of hospitality at the Fort, his account indicates that he and Nuttall were frequent and welcomed visitors. Actually for several months Townsend was placed in charge of the hospital of Fort Vancouver and he acted as physician in the absence of a regular company medical doctor. The only account of Nuttall's activities on this expedition was recorded by Townsend in his narrative. Although Nuttall kept a diary on other occasions, no diary of his trip to the Oregon Country is known at the present time. He described his plant collection of the Northwest in the *Transactions of the American Philosophical Society* in 1840. Nuttall's name is particularly perpetuated in the region by the beautiful flowering dogwood (*Cornus nuttallii*) named by the famous ornithologist James Audubon.

The greatest array of scientists to visit McLoughlin at Fort Vancouver was the members of the United States Exploring Expedition under the command of Lieutenant Charles Wilkes. The expeditionary forces had been split up in making surveys in various areas of the Pacific Ocean so that they arrived at different times during the summer months of 1841. The narrative of the expedition by Commander Wilkes contains numerous references to and descriptions of Dr. McLoughlin and Fort Vancouver. The hospitality shown Wilkes was recorded as follows:

He is a tall fine-looking person of a very robust frame, with a frank manly open countenance, and a florid complexion; his hair is perfectly white. He gave us that kind reception we had been led to expect from his well-known hospitality . . . He at once ordered dinner for us, and we soon felt ourselves at home, having comfortable rooms assigned us, and being treated as part of the establishment.

A few days later McLoughlin provided Wilkes with a large river barge, fully provisioned, so that he could adequately explore the Willamette River.

William D. Brackenridge, horticulturist of the expedition, likewise was impressed with McLoughlin, his gardens, and his orchards. Of this he wrote:

I can say but little, having spent only a few hours with the principal, Dr. McLoughlin, who in the most friendly manner showed me around his gardens.

The botanical collection of the Wilkes expedition was described by Dr. Asa Gray. One large volume of 777 pages and atlas was published in 1854 and another volume remains unpublished. The ferns and fern allies were described by Brackenridge in a 357-page volume with atlas, also in 1854.

An overland exploring expedition under Captain John C. Fremont was organized to coordinate the inland exploration with the activities of the Wilkes expedition. On November 8, 1843, Captain Fremont arrived at Fort Vancouver and in his report of the expedition recounted the meeting with Dr. McLoughlin:

I immediately waited upon Dr. McLoughlin, the executive officer of the Hudson Bay Company in the territory west of the Rocky Mountains, who received me with

the courtesy and hospitality for which he has been eminently distinguished, and which makes a forcible and delightful impression on a traveller from the long wilderness from which we had issued. . . . but every hospitable attention was extended to me, and I accepted an invitation to take a room in the fort, "and to make myself at home while I staid."

The plants collected by Fremont were described by Dr. John Torrey in 1854 in a volume of the *Smithsonian Contributions to Knowledge* and also in Fremont's report.

This account could easily be lengthened by quoting records of other acts of hospitality administered by the well-known Chief Factor of the Hudson's Bay Company. Also, it could be pointed out that McLoughlin's employees, particularly the medical doctors of the Fort, made important discoveries in botany and natural history. Their books constituted the first science library in the Pacific Northwest. However, another important contribution of McLoughlin to science must not be overlooked; his control over the native Indians which made the wild forests relatively safe for the pioneer scientific explorers.

Dr. McLoughlin, as supreme ruler of the Pacific Northwest, was a strict disciplinarian who combatted Indian crimes with stern justice. H. H. Bancroft in his *History of the Northwest Coast* described McLoughlin's unusual influence over the savage mind. Before McLoughlin's time it was not safe to travel far except in armed bands. After McLoughlin's time as Chief Factor, the history of the Pacific Northwest is marked by brutal massacres and bloody Indian wars which took the lives of many white settlers. However, Bancroft pointed out that McLoughlin:

. . . achieved by his wise and humane policy a bloodless revolution, savage foes metamorphosed into steadfast friends, a wilderness teeming with treachery into a garden of safe repose.

While much has been written of McLoughlin and thousands of people each year visit his historic home, his contributions to the sciences, particularly the botany, of the Pacific Northwest have been entirely ignored by historical writers. September 3, 1957, marked the centennial of the death of the once mighty ruler of the Oregon Country and it is proper that the scientific world take slight note of a great friend.

Portland State College  
Portland, Oregon

#### REVIEWS

*Native Plants for California Gardens.* By LEE W. LENZ. ix + 166 pp., frontispiece (color photograph), 100 halftone illustrations. 1956. Published by Rancho Santa Ana Botanic Garden. For sale at Abbey Garden Press, Pasadena, California. \$3.85.

According to the foreword: "This book is the outgrowth of a series of papers devoted to the botany and horticulture of California plants, published as the Leaflets of Popular Information by the Rancho Santa Ana Botanic Garden. An attempt has been made to select from the native flora those species which can be recommended as of value to gardeners, described them in simple language and giving their cultural

requirements as well as suggested uses in California landscaping and gardening. In order to make the identification of the plants easy for those not already familiar with them, the majority of the species are illustrated."

Four chapters set the background for the body of the book. These treat respectively the uniqueness and diversity of the California flora, early collectors, landscaping uses of natives, and procedures in garden culture. Of the four, unquestionably the information in the first chapter is the most basic for anyone not already intimately acquainted with the topography, climate, soils, and major plant communities of California. Nowhere is it more true than in transferring native plants from their indigenous environment to the artificial conditions of a garden that, "For what we obtain of *Nature*, we must not do it by commanding, but by courting of her." Although considerable information is presented, even more could have been included in the first chapter with profit.

The second chapter surveys botanical and horticultural collectors of the period 1769 to about 1906. Some readers will appreciate this information, some will pass it over. On the horticultural side one wishes the period might have been extended to the date of publication in order to have included several pioneer collectors who should not be omitted in any history of the introduction of natives to California.

The third chapter is largely a tabular cross-index to the landscape uses of those plants which are discussed in detail later in the book.

The fourth offers recommendations on propagation and handling. It is written especially for the person who is unfamiliar with both general techniques of propagation and the particular plant materials. The author has chosen to meet the needs of such a gardener by being concrete and specific rather than by developing general principles in greater detail. As with any approach there are advantages and disadvantages. Much of the data on plant materials in this chapter is a recapitulation of the information on propagation given under each species in the body of the book.

The body of the book is a formal treatment of 101 species with generous references to additional related ones. Most of the species selected are ornamentals although a few, such as *Aristolochia californica* and *Chorizanthe staticoides*, are curiosities or have only limited horticultural values. Some 50 per cent are shrubs, 35 per cent annuals and perennials, and the remaining 15 per cent are equally distributed between trees, vines and bulbs. Nearly four-fifths of the shrubs and a third of the other species are limited to the southern part of the state in natural occurrence. The caption of each species treatment includes not only scientific and common name but a figure representing maximum height — a very helpful position for this information. The material itself is organized under: Description, Distribution, Propagation, Flowering (omitted for annuals and perennial herbs), Uses, and comments (no heading). The description is botanical, that is, for identification, rather than horticultural for characterization. Distribution is stated briefly, propagation expanded. While uses refer to landscape uses, in some cases recommendations as to where in California the plant can or cannot be grown are included. The only pertinent topic one misses in the treatment of species is that of natural associates, for natives are grown most conveniently with other natives; however, some glimpse of associates will be found in the introductory chapter on the California flora. Excellent black and white photographs, chiefly the work of M. and M. Carothers, accompany the section. The author is to be congratulated on not having followed any slavish plan in the illustrations, but of letting the nature of the plant dictate how it could be portrayed most effectively.

Even though the brief literature list at the end of the book is not intended to be exhaustive, it indicates how little has been written in this field and how grateful the reader can be for the present contribution. The only serious omissions in this list are the two excellent volumes of Lester Rowntree, "Hardy Californians" (1936) and "Native California Shrubs and Their Value to the Gardener" (1939).

"Native Plants for California Gardens" takes its place on the gardener's reference shelf as the first book on California natives in the encyclopedic style, the first predominantly on natives of and for southern California, the first effort to compile

and coördinate experiences of the staff of the Rancho Santa Ana Botanic Garden of native California plants (formerly located at Santa Ana, now at Claremont, California) into one handy volume for the interested public. It presents a large amount of information in readily accessible, clearly organized form and is enhanced by excellent illustrations.—HELEN-MAR WHEELER, Department of Botany, University of California, Berkeley.

*Plant Classification.* By LYMAN BENSON. xiv + 688 pp., 399 illustrs. 1957. D. C. Heath and Company, Boston. \$9.00.

This is a notably handsome book. The nearly 400 illustrations, including serviceable diagrammatic sketches by the author, beautifully conceived and executed analytical representations of plant families by the talented late Jerome D. Lauder milk, and well chosen photographs of natural vegetation, occupy approximately as much space as the text.

The bulk of the text (more than 300 pages) is devoted to a systematic treatment of the vascular plants—dicotyledons, monocotyledons, gymnosperms, and pteridophytes, in that order. All 80 orders of living vascular plants recognized here are keyed, as are the 332 families accepted. Chief emphasis is placed upon dicotyledons, for which the author has perfected a new five-fold system stated to be based upon "relationships" but not "purported phylogeny." The principal groups are Thalamiflorae, Corolliflorae, Calyciflorae, Ovariflorae, and Amentiferae; "the Amentiferae appear to be mostly an artificial group, and they are retained as a unit because their relationships still are not settled . . . the other four are more natural than artificial." The author believes that students should build their understanding of plant relationships around a concept of how close, or how far removed, the plant in question is from the Ranales. His groupings are designed to facilitate the development of such a concept.

Each synopsis of a class of plants appears under the heading, "The Process of Identification"; it is preceded by one or more chapters entitled, "The Vocabulary Describing . . . Characteristics," which is an illustrated résumé of the gross morphology of the particular group. This feature is strikingly reminiscent of Gray's classical "Lessons in Botany," and gives especial appropriateness to the beautiful photograph of "the father of North American botany," clad in field clothes, which serves as frontispiece.

After the encyclopaedic description of each class, there follows one or more chapters on "The Basis of Classification," which comprise a rather mixed assortment. Under angiosperms there is a chapter on "Evolution," consisting largely of a formal justification of the theory, and there is also a short section on "The Development of New Taxa"—by differentiation and isolation. Further chapters discuss "Some Fundamental Problems of Plant Classification" (method of segregating taxa, relative stability of characters), a sketch of the history of plant-classification systems, a comparison of the more recent schemes, and an exposition of the bases of the system adopted by the author.

This last chapter, summarizing the work of I. W. Bailey and his associates and students as evidence for the primitiveness of Ranales, is very promising, but its effect is considerably subdued by its relegation to pages 475 to 486. Moreover, the retention of the undoubtedly artificial and reduced "Amentiferae" as a group and of such features as a wholly artificial arrangement of fruits (based upon "fleshy" vs. "dry") and of the term "pistil," which is difficult to homologize with the evolutionary modification of megasporophylls into carpels, as discussed elsewhere in the volume, further diminish the impact.

The living gymnosperms are divided among four classes: Conopsida, Ephedropsida, Gnetopsida, and Cycadopsida. Their classification, apparently based upon a résumé of their presumed geological history, contains no reference to the work of either Sahni or that of Florin. The pteridophytes are treated similarly.



The last section deals with the "Association of Species in Natural Vegetation," and gives a descriptive sketch of North American plants under nine "floras" and a short though useful bibliography. In the middle of the book is a rather detached chapter on "Preparation and Preservation of Plant Specimens." The appendix includes a guide to favorable collecting seasons in different parts of the continent and a useful glossary.

The volume, despite its many excellent features, is difficult to sum up. The stressing of keys, identification, groupings, taxonomic hierarchy, descriptions, and collection of specimens definitely places emphasis on the *materials* of taxonomy. The arrangement of major groups, despite the chapter on evolution and that on the basis for the author's preferred system, suggests that convenience takes priority over the operations of those biological phenomena which make patterns of diversity inevitable and classification feasible. The book is designed as an elementary text for college students "*without prerequisite*," and is based on the view that the path to an appreciation of the world of plants lies primarily through learning their names and positions.—LINCOLN CONSTANCE, Department of Botany, University of California, Berkeley.

*The Mushroom Hunter's Field Guide.* By ALEXANDER H. SMITH. 197 pp., 1 figure, 124 photographs. 1958. University of Michigan Press, Ann Arbor, \$4.95.

In his introduction, Dr. Smith states that since he is concerned with mushrooms most easily identified by their pictures, illustrations are the backbone of this handbook; for each species illustrated, he includes a discussion of the important field characters rather than a formal description of the species characters. In making this book a field guide, he adds that he has sacrificed scientific accuracy, but he has pointed out in the text where it can be attained. His intention has been to illustrate the mushrooms in such a way as to enable accurate recognition and emphasize the critical characters.

In my opinion, Dr. Smith has achieved his purpose—that is, to write a field guide that would enable mushroom hunters to make accurate identifications and protect them against serious errors—more completely than one could have expected in a book of this size and simplicity. No knowledge of botany is required in order to use this guide; all that is necessary is careful observation and caution in collecting, as well as compliance with Dr. Smith's recommendations to discard all specimens that do not completely fit the descriptions and to exercise care in cooking and eating. This is a handbook that can be recommended without any hesitation and without cautionary advice to the amateur collector, since the author enumerates clearly all the dangers involved in the gathering of mushrooms for the table. The book is a good size and shape for use in the field. The photographs are excellent.

The book is intended for the Great Lakes region, northeastern United States and western United States. It includes a list of fifteen species considered safe for beginners, a list of species associated with certain trees, and a seasonal list of common mushrooms. Although only about one in thirty species in the United States is included, most of the common mushrooms, the finest of the edible species, and the most dangerous of the poisonous species are discussed and illustrated. In addition, the guide includes some of the mushrooms that are poisonous only to certain people. The introductory section includes a brief account of the role of fungi in the breakdown of organic substances, their manner of growth, nutritional and moisture requirements, and mycorrhizal relationships. The structure of fleshy fungi is also discussed, as well as variation in form, precautions to take in collecting, and the nature of Latin binomial names. Instructions are given in the use of the simplified key; a glossary and a short bibliography are also included.—ISABELLE I. TAVARES, Department of Botany, University of California, Berkeley.

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